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[PLATES 1—7.]

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ON THE COMPARATIVE ANATOMY AND AFFINITIES OF  
THE ARAUCARINEÆ.

BY

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# PHILOSOPHICAL TRANSACTIONS.

## I. *On the Comparative Anatomy and Affinities of the Araucarineæ.*

By ROBERT BOYD THOMSON, *University of Toronto.*

*Communicated by Dr. D. H. SCOTT, F.R.S.*

(Received September 14,—Read November 14, 1912.)

[PLATES 1-7.]

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### 1. INTRODUCTION.

The simple anatomical structure of the Araucarineæ is variously interpreted by botanists. The group was regarded until recently as the one family of Conifers whose connection with the Cordaiteæ of the Palæozoic was at all intimate. This view of their relationship, which is by no means at present abandoned, was based chiefly on a resemblance in gross morphology of leaf and stem and on two anatomical features—the absence from both groups of any specialised resiniferous tissue in their secondary wood and the presence in both of alternate rows of hexagonal pits on the tracheids of this wood. Dr. SCOTT stands as perhaps the most convinced adherent of the Cordaitean ancestry of the Araucarineæ, in spite of the recent works of JEFFREY and SEWARD, which tend, from different standpoints, to annul the validity of the relationship between them. These investigators both recognise that the structure

of the Araucarineæ is of a very simple type, though each interprets the simplicity in a very different way. Prof. JEFFREY considers the Abietineæ the most ancient of the living Conifers and the most closely associated with the Cordaitean forms, and regards the Araucarineæ as having been derived from them in comparatively early geological times. According to his view the ancestral Araucarians\* had leaves borne on spur shoots like the pines of to-day. The simplicity of the wood structure of the Araucarineæ, too (multiseriate pitting and absence of specialised secretory tissue), is not indicative of Cordaitean affinity but has been acquired a second time from the pine alliance with opposite pitting and complex horizontal and vertical systems of resin canals. Prof. SEWARD, on the other hand, regards the Araucarineæ as derived from Lycopod stock, and in his and Miss FORD's (1906) account of the group states the evidence in favour of interpreting the simple structure of the Araucarineæ in terms of this connection. According to SEWARD's view, the simplicity of structure is an indication of primitive organisation, while according to JEFFREY's it is in the nature of a specialisation.

Moreover, JEFFREY, in reading specialisation into the structure of the Araucarineæ, and in calling in question their connection with the Cordaiteæ, has done much to permit the Lycopod theory of the ancestry of the Conifers to become the rival of the Cordaitean. This is the more evident when it is realised how imperfectly his Abietinean substitute bridges the anatomical gap between the Conifers and the Cordaitean forms—with practically no crucially important structural feature in common between them. One need only recall in this connection the contrast between the secondary wood of the two groups in such fundamentals as pitting, ray structure, and resin tissue. Indeed, the resin tissue in itself would seem to present an impassable gulf. Over this, too, JEFFREY has not attempted to construct a bridge; his theory postulates the presence of horizontal and vertical resin canals in the secondary wood of the ancestral Abietineæ, without even a suggestion as to the origin of these canals, and yet the Cordaitean forms, which he regards as the ancestors of the Abietineæ, and with which the latter are supposedly the most closely connected of the Conifers, are devoid of such structures. SCOTT (1909, pp. 653-657), in presenting the evidence in favour of the Cordaitean versus the Lycopod ancestry of the Araucarineæ, does not refer to JEFFREY's theory, which, if correct, renders the one—and possibly the greater, the constructive—part of his argument groundless. Thus, as the problem stands at present, the writer considers that any evidence that tends to overthrow the Abietinean theory of the ancestry of the Araucarineæ and to strengthen the connection of this family with the Cordaitean alliance, makes the case doubly strong against the Lycopod theory.

In the present work evidence of the phylogeny of the group is advanced from a comparative study of the structure of the different regions of the individual plant. The reproductive branches and leaves have, since Dr. SCOTT's work on the Cycads,

\* Araucariopitys and Woodworthia, JEFFREY, 1907 and 1910 *a*.



been recognised as places where primitive structure is retained. The conservative character of the root has, however, not received the attention it deserves. Again, it seems scarcely to have been recognised that anatomically the tree, from the cambium inwards, is an *adult with all the stages of its own development preserved*. These three features have been kept prominently in view throughout this study of the Araucarineæ. The work has also necessitated a comparison with similar features in other living and fossil forms, since it is recognised that in this way only can the true phylogenetic value of the evidence be estimated. The conclusion to which the results point is the association of the Araucarineæ with the Cordaitalean forms, using this term in the extended sense in which it is employed by Dr. SCOTT (1909) in the second edition of his 'Studies in Fossil Botany,' where he includes the Poroxyloæ, Pityææ, and Cordaitææ under the Cordaitales.

## 2. LEAF GAPS AND PRIMARY STRUCTURE.

The fundamental tissue of the stem consists of parenchyma elements with sclerites in both pith and cortex. In fig. 1, Plate 1, of the stem of *Araucaria imbricata* almost all the irregular spaces in the pith and cortex are bounded by the thick walls of the sclerotic cells. In some instances, however, these cells have dropped out of the section, and the spaces are bounded by the walls of the adjacent parenchyma cells. On the walls of the sclerotic cells, when seen in face view, the marks of calcium oxalate crystals are very distinct (fig. 2). WINKLER made an accurate study of these in *A. brasiliensis* as long ago as 1872, and compared them with those of *Welwitschia*. Many of the parenchyma cells have deeply staining, tanniniferous or mucilaginous contents. These cells are often associated with the sclerites. In the root the sclerenchyma cells are of regular form and are arranged in a cortical sheath just within the periderm (fig. 8, Plate 1). In the cortex there are large mucilage ducts (figs. 1 and 3), often an inner and an outer series. They occur in the cortex of the root also, but are usually not so numerous here (fig. 8) as in the stem. These ducts vary much in number in the different species, as do the sclerites, and are not so numerous in the seedling as in the adult; nor have they been found in the medulla of the former nor in that of the adult stem or branches. In the medulla of the cone axes, however, both male and female, of *Araucaria imbricata* I have found them in abundance. In the upper part of fig. 5 the more central medullary canals can be seen. The peripheral ones connect through the gap above the sporophyll traces with those in the cortex. In the figure two traces may be seen in the cortex, one (*Sp. t.<sup>1</sup>*) to the lower left, the other (*Sp. t.<sup>2</sup>*) to the right. Above the left one is a mucilage duct in the cortex, midway between the trace and the ring of bundles. It has followed in the wake of this trace as the latter withdrew from the medullary crown. The other trace has a corresponding mucilage duct, which is just in the gap between the axial bundles. The course of these mucilage ducts has been followed in radial sections. They pass rather obliquely upwards and outwards to join the cortical series and form

an anastomosing system quite comparable to that which appears in the stem of the modern Cycads. This connecting series of canals is clearly to be distinguished from the horizontal series of the pines by the fact that in the latter the horizontal resin canals do not extend to the pith, but have some secondary wood elements between them and it; they originate also in the outer wood at various distances from the pith, in connection with the increase in circumference of the stem.

The occurrence of the medullary mucilage ducts in the cone axes and their connection with those in the cortex, besides being interesting and probably phylogenetically important, from the standpoint of the retention of a primitive form of organisation (*cf.* Cycads and Poroxyton), has a bearing on the Lycopsid or Pteropsid ancestry of the Conifers. The exit of the foliar trace in the Araucariaceae leaves a gap in the central cylinder of the stem (fig. 1, Plate 1), whether these leaves be large or small, a feature which JEFFREY has demonstrated in the whole Conifer series. The continuity of the medullary and cortical sclerenchyma through the leaf gap makes this gap the more evident (fig. 4, Plate 1). The *ancestral* presence of the leaf gap in the Araucariaceae is strikingly indicated by the continuity of the medullary and cortical secretory canals in the *cone* axes of *Araucaria imbricata* above described. It is further emphasised by the presence of a leaf gap in the seedling (fig. 6, Plate 1). On this broad anatomical basis the Conifer series naturally attaches to the Pteropsid line of descent, and is precluded from the possibility of the Lycopsid connection which SEWARD's view postulates. The writer makes this statement fully cognisant of the present controversy over the extra- or intra-stelar mode of origin of the medulla, since, so far as he can see, the presence of a leaf gap in the Pteropsid line and its absence from the Lycopsid have been established, and the preponderating importance of the leaf in the former as compared to that in the latter is practically admitted by all anatomists.

The pith may be large or small in the stem of the Araucariaceae. It shows regional variations, also, in some forms at least. In *Agathis alba*, where branchlets come off the pith is large, but where these join the medullary crown the pith is much contracted, in one instance by actual measurement only 0.35 mm., as compared with 7.5 mm. There would seem also to be much variation in the diameter of the pith in different species. In most cases, however, it is large, larger than that in any other group of the Conifers. In the cone-axis of the Araucariaceae, especially in the seed cone, the pith is exceedingly large, that of *Araucaria Bidwillii* for example may attain a diameter of almost an inch. In the stem of the Cordaitacean forms there are similar variations in the size of the pith. The Poroxytons have a very small pith (1-3 mm.), while that of Mesoxylon\* is comparatively large. Of *Pitys antiqua*, SCOTT (1909, p. 515) says: "The imperfectly discoid pith is large, sometimes as much as 2 inches across," while of Cordaites he states (p. 523) that the pith cavity is "sometimes very slender, but usually an inch or more, and sometimes approaching

\* SCOTT and MASLEN, 1910.

4 inches in diameter." I have examined the size of the medulla of the stem and cone-axis (seed cone) of many of the Abietinæ, but have found nothing to compare with the size of that in the Araucarinæ, though the pith of the cone is considerably greater than that of the stem. In the variability in the size of the pith, and in the magnitude which it may attain, the Araucarinæ are the only forms of the Conifers at all comparable to those of the Cordaitalean alliance.

In the pith of a stem or branch of *Agathis australis* I found that the sclerenchyma forms practically a solid mass. (See fig. 53, Plate 6, and discussion in Section 6.) In the cone of this form, however, the sclerotic tissue is grouped in little masses, which recall the "sclerotic nests" of Lyginodendron. As in the latter, too, they project into the sporophyll gaps, and form, as it were, a continuation of those in the cortex. The pith is never discoid in the Araucarinæ, as is typically the case in Mesoxylon and the Cordaitæ, but agrees with the Poroxyleæ in this respect. Between the extremes in the Cordaitalean forms the Pityæ occupy an intermediate position, the pith being imperfectly discoid in this family.

The primary wood of the root is usually in the form of a diarch plate (fig. 8, Plate 1), but in some cases a triarch structure has been observed.\* The protoxylem is often separated by several parenchyma cells from the metaxylem (fig. 9). Its elements are massed, and have no indication of the "forked" condition of the *Pineæ*, where a resin duct separates the two "tines" of each arc of protoxylem; nor is there any indication of a resin duct in the centre of the metaxylem, as is characteristic of the *Abietæ*. The latter may either be solid (fig. 9) or with parenchyma interspersed among the xylem elements. In most cases there is a series of parenchyma cells surrounding the whole primary wood and separating it from the secondary, but in *Agathis Moorei* I have observed that sometimes the primary and secondary elements come into contact with one another. The character of the protoxylem in longitudinal section is illustrated in fig. 10 (Plate 1). The central strand here consists altogether of protoxylem. To the left is some metaxylem. Fig. 11, Plate 2, illustrates the various conditions of pitting of the latter. In only one place is typical alternating hexagonal pitting present. The chief type is what might be called transitional scalariform, *i.e.* scalariform which shows signs of becoming typical multiseriate bordered pitting. The elements of the primary wood of the root are usually quite long, but I have observed that where a lateral root is given off they may be considerably shortened (left of fig. 12, Plate 2, with lateral root attaching at the upper right of the figure). These elements are continuous with the ordinary elongated ones and form an interesting parallel to the condition in the leaf, where most of the centripetal xylem is short and of the transfusion tissue type. The elements nearest the protoxylem, however, are always long in the leaf. In the stem, as is usual in modern forms, the boundary between the primary and the secondary wood is not distinct, the French school of anatomists speaking of

\* SEWARD, 1906, p. 338.

the whole of the first year's growth as primary. Around the pith of the stem are essentially the same kinds of elements as are found in the primary wood of the root. The innermost elements of this so-called "medullary crown" are ringed and spiral, and in sequence with them are scalariform and typical multiseriate pitted elements. The transitional area in the stem is a very broad one, the one type of element giving place very gradually to the other. This is a feature to which both PENHALLOW (1904 and 1907) and SEWARD (1906) have referred, and they evidently agree on its Cordaitean interpretation. Especially significant, however, is the broad transitional zone of the cone-axis (fig. 32, Plate 4). This is as broad, or even broader, than that in the stem of any of the Cordaiteæ. In no other group of the Conifers is there an approach to this Cordaitean condition.

### 3. LEAVES.

#### a. *Leaf Morphology and Habit.*

The leaves of the Araucarineæ vary considerably in form but much more in size. The variation occurs chiefly in the genus *Araucaria*, though the largest leaves in the group belong to species of *Agathis*. The leaves of the latter are lanceolate to ovate or elliptic lanceolate, often contracted into a petiole at the base but sometimes sessile. I measured two leaves from specimens which were sent me from the Buitenzorg Botanic Gardens. One, labelled *Agathis Dammara* Rich., was  $12.5 \times 3.5$  cm. and had a petiole 1 cm. long. The other, of *Agathis Bidwillii* Hook., was  $11 \times 4.25$  cm., with petiole 0.75 cm. SEWARD (1906, p. 315) refers to LINDLEY's description of *Agathis macrophylla* as being 17 cm. in length and 5 cm. in width. This is the largest leaf of any species of *Agathis* to which the writer has found reference, and in shape and size affords the nearest approach on the part of the living Conifers to the Cordaiteæ, of which RENAULT (1879, p. 296) says: "Les feuilles de Cordaïtes sont de dimensions très différentes: il y en a de 12 centimètres, jusqu'à un mètre de longueur, sur une largeur qui peut atteindre 20 centimètres." In *Araucaria* the base of the leaf is always broad, often the broadest part, and a petiole is never present. The leaves may be large, broad, and flat as in *Araucaria imbricata*, or small, narrow, and falcate as in *A. excelsa*. Since the cotyledons are broad in *Agathis*, and generally so in *Araucaria*, and have several veins, the large size is probably primitive.

The leaves are persistent from several to very many years, more so in *Araucaria* than in *Agathis*. SEWARD (1906) states: "In some cases stems (of *Agathis*) apparently 10 years old retain functional leaves" (p. 311), while in certain species of *Araucaria* "the leaves remain on the tree for 10 or even 15 years" (p. 318). In both genera they are often not shed individually but by the dropping of lateral branches when these are several years of age. One can observe this very readily in any greenhouse specimen of *Araucaria excelsa*, and Dr. A. J. EAMES tells me that it is quite characteristic of many species in their native haunts (e.g. *Agathis australis* and *Araucaria Bidwillii*) which came under his observation on a recent Australian

and New Zealand trip. This interesting feature suggests the deciduous spur shoot of our pines. Though the latter are very specialised structures (see Section 9) as they occur in the living pines, when one considers that they have come from forms in which these shoots were practically small branches with numerous leaves (Prepinus of the Cretaceous), and that at first the branches were persistent (Woodworthia of the Triassic), one sees how close the parallel really is. Our pines, however, must have come from forms which had a branch in the axil of every leaf, and the living Araucarinæ fail in this respect, though the deciduous branches are more numerous than in any other group of the Conifers. The recently described *Mesoxylon Sutcliffii* is a form which has in it the possibility of meeting this, since every leaf so far observed has a bud in its axil.\* In *M. multirame*† there is a branch in the axil of nearly every leaf. The deciduous branch is one method by which the Conifers overcame the persistent foliage habit of the ancestral forms, when adapting themselves to more modern climatic conditions. The other and more usual was by the foliage itself becoming deciduous, as it has done to a marked degree in all the other Conifers except the Araucarinæ, and even to some extent in all these and to a great extent in many of them. That the persistent habit is the ancestral one in the Araucarinæ is clear from two facts. For one, I am again indebted to Dr. EAMES, who has observed that the leaves persist longer on young than on mature trees. This is the more evident in those species whose mature leaves persist for only a very few years (e.g. *Agathis australis* and *Araucaria Bidwillii*). The other point is the practically indefinite persistence of the leaf trace (see Section 3c) in the Araucarinæ, especially significant being its persistence in the forms which shed their leaves comparatively early.

There is also evidence that the persistent habit is the ancestral one in the other modern Conifers. In the deciduous forms, e.g. *Larix*, the leaves remain attached in the young plant for several years, and in the ordinary evergreen species there is an accentuated persistence of the leaves in the young forms and on the main axis as well. Another indication is in the persistence of the leaves on the spur shoot. In the living pines the foliage may clothe the branches for 10–15 years.‡ Especially does the shoot remain long attached on the main axis of the vigorous young plant. When we turn to the fossil forms, it is unfortunate that the data are incomplete. The spur shoots of Prepinus of the Cretaceous§ have been found only in the detached condition, and hence the duration has not been determined. In Woodworthia (Triassic), on the other hand, we have no proof as to the persistence of the leaves on the spur shoot, though the shoot itself is considered to remain on the trunk for fifty years or more,|| a point which has been inferred

\* MASLEN, 1911.

† SCOTT and MASLEN, 1910.

‡ E.g. *P. Balfouriana*, KENT, 1900, p. 30.

§ JEFFREY, 1908, 1910 b.

|| JEFFREY, 1910 a.



from the presence of its trace, though the shoot itself is unknown. If this is a true spur shoot homologous with that of the pines, it must be assumed that the leaves persist as long as the shoot itself.

The persistent condition is thus the ancestral one for the Conifers, and the Araucarineæ take precedence over all the others, not only in respect to the greater persistence of their leaves, but also in probably being the only living forms with indications of the two processes by which the persistent habit has been overcome, by the *deciduous leaf* and by the *deciduous branch*. With respect to persistence, the leaves of the Araucarineæ resemble those of Cordaites, where they are very persistent, since they are represented as attached near the base of old branches.\* I can find, however, no definite reference to this feature in the fossil literature, probably because of the detachment of the leaves by the exigencies preceding and attending fossilisation, which make it difficult to determine how long they really did persist. GRAND' EURY (1877, p. 266) does, however, make a definite statement with regard to the branches. He says that they are only occasionally found on old wood but very numerous on young stems, from which he infers that many of them must have fallen early. This is a curious parallel to the Araucarians, and not only is there a parallel in the deciduous branch habit but in the character of the branching. In both groups the branches often come out high in the axil of the subtending leaf. The branches, too, may be variable in size, and only exceptionally in Cordaites do they come off in verticils.

Another feature in connection with the leaf of the Araucarians is the persistence of its base. This is much better developed in Araucaria than in Agathis and remains green for many years in some cases, and, together with the leaf or the remains of it, forms a protective outer coat to the stem.† The "armour" of the Cycads consists of just such leaf-bases and disorganising leaves, but has alternating with them a series of scale leaves.

The Araucarineæ with large leaves resemble Monocotyledons with numerous parallel veins. The small-leaved forms have only a single vein. SCOTT (1909, p. 654), in deciding on the ancestral type of leaf, says: "That the multinervate character is primitive (in the Araucarineæ) is indicated by the fact that the cotyledons likewise contain several bundles." The force of this is very evident when one considers such a form as *Araucaria excelsa*, where the adult foliage is so much reduced that there is only a vestige of the multinervate condition in the leaf trace as it passes through the cortical region of the stem. Here two small and very short lateral branches are given off from the single central bundle, which alone continues into the lamina. In the large cotyledons of this form there are several distinct veins.

TISON (1912) has recently devoted some attention to the character of the venation in all the Conifers and has shown that dichotomy is a more widespread phenomenon

\* See SCOTT, 1909, fig. 187, after GRAND' EURY.

† See SEWARD, 1906, Plate 23, fig. 6.



than was thought. He studied representatives of the different groups and has found evidences of dichotomous venation in all, either in the vegetative leaves or in the cone scales, fertile and infertile. In the leaves of *Agathis* and *Araucaria* this ancient form of venation is well marked, and TISON makes the comparison of the venation of these forms to that of *Cordaitea*, citing *Agathis obtusa*, which he says is identical with the latter.

b. *Leaf Structure.*

Besides showing an approach to the *Cordaitea* in size, form, habit, and venation, the leaves of the Araucarineæ present certain structural points of resemblance to this fossil group. The leaves of both are tough and leathery because of the amount of hypodermal sclerenchyma which is present. This is especially abundant on the upper side and towards the apex of the Araucarian leaves, where it assumes the form of strands, for example, in *Araucaria brasiliensis* (fig. 14, Plate 2), quite comparable to those of one form of *Cordaitea* described by RENAULT (1879, fig. 3; Plate 16; or reproduction in SCOTT's 'Studies,' fig. 192A). The palisade consists of several series of cells in *Cordaitea*.\* These cells are little differentiated, slightly longer than broad, and arranged very indefinitely. In *Agathis Moorei* (fig. 13, Plate 2) there is a palisade with two or three rows of cells. These are short and variable in form. They are filled with very dense black homogeneous contents. In the leaf of both groups there is a relatively large amount of spongy parenchyma which below the palisade cells may show considerable lateral elongation.

With regard to centripetal xylem and "intrastelar" transfusion tissue, the writer's work has led him to practically the same conclusion as that which has been reached by both WORSDELL (1897) and BERNARD (1904), the two recent investigators whose work on these features in the Gymnosperms has been both thorough and extensive. *True centripetal xylem* is *opposite the protoxylem*, and the writer wishes to draw attention to the bearing of this point on the interpretation of the leaf bundle of the Araucarineæ. The transfusion tissue is attached to the flanks of the centripetal xylem when, as in the leaf and petiole of the Cycads, there is much primary wood present. On the loss of the primary wood in the higher forms, and its replacement by secondary wood, the transfusion elements become laterally continuous with this. Typical transfusion tissue may thus be attached to the centripetal primary wood or to the secondary, as the case may be. In the Araucarineæ both conditions are present. When we follow the vascularisation from the base of the leaf upwards, the first transfusion tissue which comes in is attached to the sides of the secondary xylem, which up to and beyond the middle of the leaf constitutes practically the whole ligneous part of the bundle.† Gradually, farther towards the apex, the two wings of transfusion tissue are united by xylem elements above the secondary wood. This part opposite the protoxylem is true centripetal xylem. It increases gradually

\* RENAULT and SCOTT, *l.c.*; STOPES, 1903, figs. 1 and 7, Plate 9.

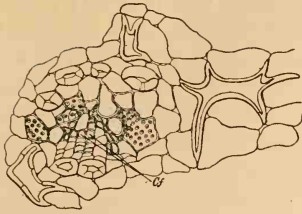
† In this statement I have omitted the centrifugal primary wood because of its unimportant character.

towards the tip of the leaf, where there is a complete replacement of the secondary wood of the bundle by it and the transfusion tissue. (See text-figures 1-4, which are taken from BERNARD, and compare with figs. 13 and 14, Plate 2. Fig. 13 is from the middle of the leaf, and its vein shows no true centripetal xylem, while fig. 14 is from the apex and has an enormous amount.) The vascular bundle in the apex of the leaf resembles that of the Cycad petiole or leaflet, where there is only a trace of secondary wood, or none. This recently demonstrated occurrence of true centripetal xylem towards the apex in Araucarian leaves makes their association with Cordaites in internal structure, as well as in external form, a very intimate one.

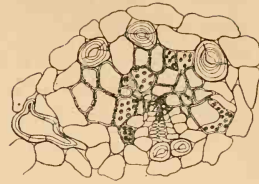
This view of the centripetal xylem is held in spite of the fact that JEFFREY in his work on Cretaceous pine leaves does not consider the tracheary tissue opposite the protoxylem in the living Conifers to be centripetal xylem. He says (1908, p. 218): "It seems much more highly probable, from the conditions observed in Prepinus and in species of Cretaceous Pinus, that such elongated elements with bordered pits are in reality vestiges of the ancestral inner transfusional sheath (of Cordaites), the real centripetal xylem having disappeared at too early a stage to be represented even vestigially in living Conifers." FUJII, on the other hand, has recently called attention to some of the anomalies of the centripetal xylem of Prepinus. He states (1910, p. 204): "It may be a question whether any tracheal elements on the ventral side of a centrifugal xylem developed regularly, in direct continuation with a medullary ray of a stem or a medullary plate of a leaf in the same plane with the latter, and not starting from one of the protoxylem elements, can be taken for elements of a centripetal xylem." In the arrangement in rows of the centripetal xylem of Prepinus and in the alternation of these with the strands of broken down protoxylem he finds no parallel in any true centripetal xylem. It is certainly very different in these respects from that of the Cycads and of *Cordaites principalis*, to the latter of which JEFFREY compares it. In the Cordaites form the centripetal xylem is continuous with the protoxylem and shows a depth of not more than two or three elements, whereas in Prepinus the centripetal xylem alternates with the protoxylem and attains a much more extensive development, reaching a depth of six to eight elements.

Aside from the morphological peculiarities of the centripetal xylem of Prepinus, if amount means anything phylogenetically, the greater amount in Prepinus as compared with its Carboniferous prototype must be explained, if this tissue in Prepinus is true centripetal xylem. FUJII (1910) has found, however, in two living pines, *Pinus densiflora* and *P. Thunbergii*, a quite comparable though much less extensive centripetal xylem of the Prepinus type. Moreover, there are difficulties in the way of JEFFREY's interpretation of the centripetal xylem of the Araucarians as vestiges of the inner transfusion sheath. In Cordaites, this arches over the phloem of the bundle connecting only with the flanks of the centripetal xylem,\*

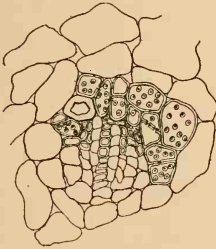
\* STOPES, 1903, fig. 5, Plate 9.



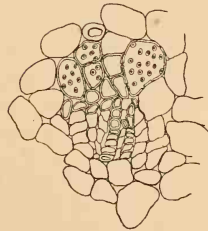
TEXT-FIG. 1 a.



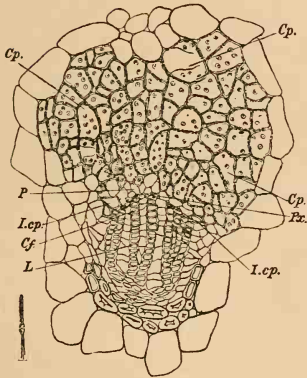
TEXT-FIG. 1 b.



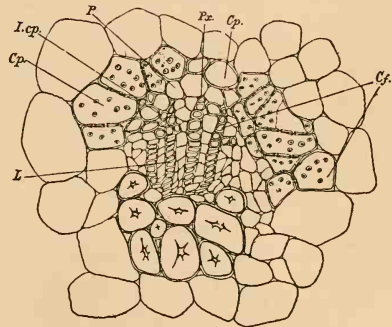
TEXT-FIG. 2 a.



TEXT-FIG. 2 b.



TEXT-FIG. 3.



TEXT-FIG. 4.

Illustrations of Centripetal Xylem in the Araucarinææ, reproduced from BERNARD.

Figs. 1 a and 1 b, *Agathis loranthifolia*. Both from near the distal end of the leaf, showing well developed centripetal xylem and transfusion tissue, and very little secondary wood. Figs. 2 a and 2 b, *Agathis australis*. The former is from the middle of the leaf and shows less abundant and less typical centripetal xylem. Fig. 3, *Araucaria imbricata*. An enormous mass of centripetal xylem is present. Fig. 4, *Araucaria Bidwillii*. True centripetal xylem of small amount.

and it is in this form, or some modification of it, that it should appear in the primitive region of the Araucarineæ. On the contrary, it is centripetal in the terminal, more primitive portion of the leaf, while in the middle it flanks the bundle. In the cotyledons, too, it is of the former type.\* Further, JEFFREY's view of the origin of the centripetal xylem of the living Conifers involves the loss of what he regards as the true centripetal xylem and the replacement of it by similar elements of the inner transfusion sheath. Even granting the possibility of this, the demonstration of it would be exceedingly difficult, and has not been attempted. Until some evidence is advanced other than the anomalous centripetal xylem of *Prepinus*, it is better to regard the centripetally placed wood elements of the Conifers as true centripetal xylem. However, so far as the comparison of the leaf of the living Araucarians with that of the Cordaites is concerned, there are other Cordaitan forms with true centripetal xylem and no inner transfusion sheath, and it is with these that the Araucarian leaves may be compared.

### c. Leaf Traces.

In recent years there has been an enormous importance attached to the leaf trace from the phylogenetic standpoint. Reference has been made (Section 2) to its now generally recognised value as a criterion in distinguishing the two great phyla of the vascular plants, the Lycopsidea and the Pteropsida. To the character of the trace, whether single or double, much attention has also been given by recent investigators. With regard to this point, there would seem to be a difference of opinion as to the region in which the single or double character of the trace is of significance. Many botanists regard the ligneous zone as the important place. On the other hand, JEFFREY (1905) makes the cortical region the centre of his investigations on the Abietineæ. Since the traces come from the primary wood in the medullary crown, and are continued through the cortex into the petiole and leaf blade, it would seem that they should be studied from their origin at the pith to their final ramifications in the lamina.

In radial section the course of the leaf trace of the Araucarineæ is obliquely vertical from its position in the medullary crown through the first two to three years of secondary wood. After this it pursues an almost horizontal direction, no matter how large the trunk may be in which it is found. It is so horizontal that I was able to follow with a hand lens a small trace of *Araucaria Cookii* on the end of a log, from near the pith to the cambial region, a distance of 15 cm. The horizontal course of the leaf trace through the great extent of secondary wood is characteristic of the Araucarineæ. Beyond the wood in the inner cortical region the direction of the trace becomes almost vertical, and in the forms, the leaves of which are situated far apart on the stem, the cortical extent of the trace is of corresponding length. In the outer cortical region they gradually revert to the

\* WORSDELL, 1897, fig. 17, Plate 26.

horizontal on passing into the leaf base. Their further course and dichotomous branching in the lamina of the leaf have been fully described by TISON (1912), as indicated in a previous paragraph. Reference will also be made to these points later.

The traces vary in size in the different forms, and even the individual trace is not of uniform size in its course through the secondary wood. Those of such forms as *Araucaria excelsa* are the smallest, while the largest I have come across are of species of *Agathis* in very old wood. The double trace was first observed in old wood of *Agathis australis*, and because of the large size of one of its components it was thought that this might be the trace of a branch, and the other the leaf trace in the axil of which it arose. To satisfy myself that the double trace really belonged to the single leaf, I followed the pair in a younger stem from the leaf base into the secondary wood. The leaf trace, moreover, is quite readily distinguishable from that of the branch, since the wood of the branch makes usually a circular, always a lateral, attachment to the secondary wood through which it is passing; while in the leaf there is a large basal and very little other attachment.

My results on the study of the persistence of the leaf trace in *Araucaria* agree with and supplement the conclusion arrived at by SEWARD and FORD (1906, p. 353). I have followed the trace through wood of *A. Cookii* from a trunk section of about 30 cm. diameter. A branch of *A. Bidwillii*, with about fifteen growth-rings, showed beautifully the complete spiral sequence of the leaves on removal of the bark. In slightly older branches of *A. Cunninghamii*, the series were closer, but just as complete. In both species I have found the trace in mature wood. The bulk of its tissue is then sclerenchyma. The traces of *A. Rulei* appear in a close spiral on branches four to five years old. No wood of *A. imbricata* over fifteen years old was available, but up to that time the traces were all complete and well preserved. The wood of this species which Sir WILLIAM THISELTON DYER (1901) examined was from a trunk 1 foot 4 inches in diameter, with 60 growth-rings, and his figure shows a complete series of single traces in this old wood. TISON (1903) has described the persistent trace in *A. brasiliensis* in wood 25 years old. The trace in the genus probably persists indefinitely, whether the species has large leaves or small, and whether the leaves remain long attached to the stem or are cast comparatively early. In *Agathis* I found traces in a great number of species in wood up to about 15 years of age, but examined only old wood of *A. australis* and of *A. robusta*, where they were present in wood whose annual rings were very flat. My block of *A. robusta* was small, and I only found one bundle. In the case of *A. australis* several were observed, and the wood, judging from the convergence of the bundles, must have been from a trunk at least 30 cm. in diameter. In both genera of the Araucarineæ the leaf trace thus persists in very old trunks, probably in all species and, since the leaves fall in some of the forms comparatively early, the trace persists for many years after the fall of the leaf.



Most anatomists consider the persistence of the leaf trace in the Araucariaceæ a palingenetic feature. For example, SEWARD (1906, p. 386) refers to it as "an example of the retention of structures no longer essential to the living tree, a character which may be regarded as inconsistent with a more highly organised and more delicately adjusted type"; and cites, for comparison, the case of the Lepidodendree, where he considers that "the leaf traces persist through secondary wood of considerable thickness" (p. 397). JEFFREY (1910), however, looks upon the persistent habit as cenogenetic, but has reserved his reasons, and so only one side of the question can be dealt with. The writer, while agreeing with SEWARD, regards the habit of the leaf trace more as an index of the habit of the leaf and its greater persistence as an indication of the persistent foliage habit of the ancestral forms. This habit was characteristic of the lowly organised forms of the Palæozoic, and was superseded by the deciduous in the more highly organised types, on the advent of "winter" in comparatively recent geological times. The persistent leaf trace is thus an indication of primitiveness.

There is little evidence in the literature at present of the persistence of the trace in the secondary wood in the Cordaites. WILLIAMSON has figured some double traces in the Coal Measure forms which he described (1877, figs. 44 and 48, Plate 8, and 46, Plate 9), but was mainly concerned with their course near the medullary crown, and has only figured them in secondary wood four to five years of age. Recently, they have been shown\* to exist in old wood of the so-called *Pityoxylon chasense*, where, curiously enough, they had been mistaken for resin canals, and were regarded by PENHALLOW as the basis for referring this otherwise Araucarian or Cordaites form to the Abietineæ. I have also found traces in a specimen of *Araucarites* (so labelled in our collection, but without data as to its horizon), whose trunk measures about 15 cm. in diameter. That the trace does persist is shown by the cases above cited, and by the fact referred to before, that the Cordaites leaves remained long attached to the stem (see Section 3A), these forms belonging to the geological period when the deciduous habit had not been attained. That they have been overlooked in mature fossil wood is not strange, since they are difficult to observe, and even in the living forms have not been recognised until recently. The writer believes that many more fossil forms with persistent leaf traces will be found when the importance of this feature is realised.

There is another point in connection with the leaf traces that indicates their primitive character. STRASBURGER (1891, p. 106) has drawn attention to the fact that in the pines the resin canals in the leaves do not connect with those in the cortex, and considers this a specialised condition. JEFFREY (1908 and 1910 *b*) agrees with him, and shows that in *Prepinus* there is such a connection, and that this form is therefore of a more primitive type than the living pines. In the Araucariaceæ, the

\* THOMSON and ALLIN, 1912.



resin canals of the cortex accompany the leaf traces on their course through the base of the leaf, and connect with those in the lamina.

The leaf trace of *Araucaria* begins as a single bundle at the pith in *A. Bidwillii*, *A. Cookii*, *A. Cunninghamii*, *A. excelsa*, and *A. imbricata*, and never branches, so far as I have observed, in wood up to 15 to 20 years of age. Fig. 15, Plate 2, illustrates the single trace of *A. imbricata* in wood about three years old as it appears in tangential section. In old wood of *A. Bidwillii*, *A. Cookii*, and *A. Cunninghamii*, the trace is still single, but consists mainly of sclerenchyma. Since the trace remains single in these three species, this is probably the case in the whole genus. That of *Agathis* is usually double (fig. 16, Plate 2), and may even in some species have secondary wood ( $x''$ ) separating its two parts ( $b^1$  and  $b^2$ ) very close to the medullary crown (fig. 17, Plate 2). It is comparable in this respect to *Mesoxylon Sutcliffii* (fig. 18A, Plate 2), which has recently been described by SCOTT\* and MASLEN (1910 and 1911). In the latter, however, the components of the trace approach the medullary region together, while in many forms of *Agathis* one precedes the other (fig. 21, Plate 3). This is true of the seedling of *A. australis* also (fig. 23, Plate 3). Though the double trace is characteristic of *Agathis*, there are exceptions. I have found double traces in *A. alba*, *A. australis*, *A. Bidwillii*, *A. Moorei*, *A. obtusa*, *A. ovata*, *A. pumila*, *A. robusta*, *A. spinulosa*, and *A. vitiensis*. In some instances it is single, as in *Araucaria*, while in others it is multiple. No more than two bundles of the latter ever extend to the pith, however, so far as I have observed. The supernumerary strands are derived from these further out in the secondary wood. I have found triple traces in *A. australis*, *A. Moorei*, *A. Bidwillii*, and *A. pumila*. The case of *A. Bidwillii* was peculiar, in that the triple trace was found in association with an abortive branch, where evidently the vascular tissue of a leaf had become embedded in the branch to which it was attached. In *A. pumila* the greatest variation was found, single, double, triple, and quadruple (fig. 19, *a, b, c, d*, Plate 2) traces being present.

In this species I thought I had an explanation of the single trace, since the leaves, judging from their persistent bases, were much smaller in the region where most of the single bundles occurred. When, however, four traces (fig. 19, Plate 2) were found for one medium-sized leaf, this explanation would not hold. Again, the double trace cannot be due, as might be expected, to the breadth of the attachment of the leaf, since the leaves of *Agathis* are much narrower than those of *Araucaria*, and are even petiolate in many forms, nor is it in the broad-based forms of *Agathis* that the trace is double. The clue is probably in the character of the venation, and especially in the form of division which the trace undergoes in the inner cortical region. (*Cf.* upper trace, fig. 6, Plate 1, and lower right, fig. 22, Plate 3.) As pointed out by TISON (1912, p. 34), two dichotomous divisions of the single bundle

\* The section from which the photograph was taken was prepared for me, with Dr. SCOTT's kind permission, by Mr. LOMAX before the description of this form was published.

occur very rapidly in *Araucaria*, and the medial bundle of the so-called "false trichotomy" continues as the middle vein of the leaf, the outer bundles dichotomising to form the lateral veins of the broad-leaved forms. Fig. 22, Plate 3, is of *A. Bidwillii*, and illustrates traces with one, three, and five bundles, the central large and persistent. In the small-leaved forms, e.g. *Araucaria excelsa*, there may be only three veins formed, the two lateral of these disappearing in the cortex and the medial continuing into the lamina. In the ordinary forms of *Agathis* with the double trace, the branching of each trace is dichotomous, and the second dichotomy does not follow nearly so rapidly on the first as in *Araucaria*, nor is there any mid-vein to the leaf. I have not examined the cortex of *Agathis* with a single trace, but consider it probable that the persistence of the single or multiple condition is related to the mode of division of the trace bundle, a false trichotomy possibly leaving the central bundle persistent as in *Araucaria*.

If dichotomous venation is an indication of primitiveness, as there is every reason to believe,\* its persistence to the pith in *Agathis* makes this form more primitive in this respect than *Araucaria*, where the first dichotomy appears in the cortex. In support of this, it may also be urged that the cotyledonary traces are double in both *Agathis* and *Araucaria*. In the former, too, these traces are farther apart (fig. 23, Plate 3) than they are in the case of the mature foliage at the same distance from the pith. See, for comparison, fig. 16, Plate 2, of *Agathis spinulosa*, and fig. 21, Plate 3, of *A. Moorei*, where they are farther apart in the young stem than they are in any other species examined. Whether or not this is considered sufficient proof that the condition of the trace in *Araucaria* is a modification of that in *Agathis*, it is evident that in no other group of the living Conifers is there anything like so close an approximation to the double trace of the Cordaitalean forms as has been found in the Araucarineæ. WILLIAMSON compared the double trace in the stem of certain Cordaitalean Coal Measure forms (1877) with that in the spur shoot of *Ginkgo*, a comparison which has become classic, but one which must give place to that with *Agathis*, where the trace is double in the stem wood itself.

JEFFREY (1905) has emphasised the importance of the cortical double trace of the Abietineæ. We have in the Araucarineæ cortical traces, with eight, or even more, strands produced by dichotomy. Further, if the character of the trace were determined in the wood, no Abietinean could be put in the same class with the Araucarineæ, for none have leaf traces with a vestige of duplicity in this region. When it comes to the presence of multiple traces in the secondary wood, there is not the slightest evidence which would support the superior antiquity of the Abietineæ. Those of *Agathis*, however, find complete parallel in the Cordaites, for, besides the forms with double traces above referred to, RENAULT† has described a form, *Metacordaites Rigolloti*, with five bundles to the leaf trace, and I have found

\* See THOMAS (1907) for an explanation of the double trace in relation to dichotomy.

† 1896; see also SCOTT, 1902, p. 359.

six in *Dadoxylon Brandlingii*. One of the six is represented in fig. 20, Plate 2, and is very similar to the trace of *Araucaria imbricata* (fig. 15, Plate 2).

When to the evidence of the leaf trace is added that of the other features described above, size, form, habit, venation and structure, the ancient character and Cordaitan affinity of the Araucarian leaf are unquestionable.

#### 4. RADIAL PITTING OF THE SECONDARY TRACHEIDS.

##### a. *General Features.*

The pitting on the tracheids of the secondary wood of the Araucarinæ has long been recognised as resembling that of the Cordaitæ, though, as stated at the outset, its homology with the latter has recently been called in question.

The pitting of the Cordaitalean forms is very variable. In the lowest of these and in the Pteridosperms the pits cover the whole radial surface of the tracheids and are multi-seriate. In *Dadoxylon* the pitting is of this character only in the recognised lowest forms, while in the higher ones the pits are absent on parts of the wall. *D. Newberryi* has been given specific rank by PENHALLOW (1900) on account of the grouping of pits in little areas, while in such forms as *D. materiarium* the pits may be practically confined to the ends of the tracheids (fig. 27*a*, Plate 3). Usually they are alternate in arrangement, but I have found them opposite, especially in the terminal part of the tracheid of such forms as show a reduction in the pitting on other parts (e.g. *D. materiarium*, fig. 27*a* and *b* at X). The pits, too, of the Cordaitan forms are often not flattened by mutual contact, but may even be separated where their number is being reduced, by considerable space. In making comparison between the pitting of the Araucarinæ and the Cordaitæ usually only the multi-seriate character of the pitting and the flattened form of the pits have been taken into account.

In the Araucarian forms the pitting is much reduced in the mature stem wood, and occurs mainly at the ends of the tracheids, a feature to which STRASBURGER (1891, III) has called attention in other Conifers. Isolated pits are not uncommon (top of fig. 37, Plate 4). In the root the pitting is not nearly so limited in distribution or amount as in the stem. In the axis of the seed cone the pits extend from end to end of the tracheids (fig. 30, Plate 3; 31 and 32, Plate 4) and in *Araucaria Bidwillii* may become as much as five-seriate (fig. 34, Plate 4). The pitting in the cone is thus very similar to that of the ancient forms of the Cordaitales and the Pteridosperms. It is very different from that which one would expect to find in these regions if the Araucarians had come from an Abietineous stock. Indeed, in the primitive regions of the latter forms there is a considerable amount of resemblance to the Araucarians. Instead of the opposite pitting, the pitting in the cone axis and early wood of the Abietinæ has characteristically either scattered uni-seriate pits or bi-seriate ones which are alternately arranged. Sometimes even these pits are flattened by mutual contact.

Fig. 36 is from the root of *Larix* and shows multi-seriate pitting (*a*) which is sometimes flattened (*c*). SCHACHT drew attention to this feature as early as 1862, but in late years its significance seems to have been overlooked.

In the Podocarp group of the Conifers there are even more distinct indications of relationship to the Araucarian forms. In the root of *Saxegothæa* near the primary wood the pitting is bi-seriate,\* and here again the pits are sometimes flattened by mutual contact. Further out they become uni-seriate. I have not had the opportunity of examining any root wood of *Microcachrys* and *Dacrydium*, but in the root wood of *Podocarpus* a similar character of the pitting is present, though not to so marked a degree as in *Saxegothæa*. It is significant that in respect to the character of the pitting the Podocarp and Abietinean lines are to be associated ancestrally with the Araucarian, and the former much more intimately than the latter.

The so-called ray pitting of the tracheids, that is, the pitting where the tracheid comes into contact with the medullary ray cells, has been given considerable attention by anatomists in recent years and is recognised as an important diagnostic feature. In mature wood of the Araucarineæ this pitting is multi-seriate even when that on the adjacent part of the tracheid is much reduced or absent (fig. 26, Plate 3). Sometimes, too, the pits are flattened as they are on the other parts of the tracheid. In every instance I have found the pit with an obliquely placed oblong pore. This is its character also in the cone where even the ordinary pitting has pores of this type (fig. 34, Plate 4). The oblong pore is a vestige of the scalariform condition, and as such is an indication of primitiveness. The ray pitting in mature wood is thus of a more primitive type than that on the rest of the tracheid. The evidence of this will be more convincing after a consideration of the pitting in young wood.

Attention was long ago called to the transition between scalariform and typical multi-seriate bordered pitting in the Cycads, and PENHALLOW (1907) has shown that this feature is clearly marked in the Cordaitan forms, whose wide transitional zone he compares to that of the Araucarineæ. In the latter, at the region of transition from scalariform to typically bordered-pitted wood elements, there is a longer retention of the scalariform character where the tracheids touch the ray than elsewhere (figs. 24 and 25, Plate 3). The transition between the types of pitting, too, is more gradual, and often, especially in the root (fig. 28, Plate 3) and cone (fig. 30, Plate 3), one finds transitional features fairly far out in the secondary wood. Even in older wood two ray pits may often be found "fusing," as it is ordinarily called, but really showing reversion to the scalariform type (fig. 29, Plate 3, about the middle of the figure). The ray pits are of the unilateral bordered type (fig. 56, Plate 6, at *a* and *b*), and though nearly equal to the ordinary pits at the pith are much smaller in older wood (fig. 26, Plate 3). The accentuated scalariform condition in the cone (fig. 33, Plate 4) and the retention of this type of ray pitting in the Araucarineæ in the young wood of stem and root is a contrast to the condition in the pines. BAILEY (1910) has

\* STILES, 1908 and 1912.

shown that in the primitive regions of pine wood there are not the "Grosseporen" that characterise the old wood, but that these result from the fusion of smaller pits (piciform) like those on the other parts of the tracheids.\* The absolute proof of this is the presence in these large pits of several tori at the centres of the fusing pits, a point which seems to have escaped Mr. BAILEY. The ray pitting of the tracheids of the pines is of a specialised type, and even in its primitive (piciform) condition affords a striking contrast to the scalariform type which characterises the Araucarian in the same regions.

The Cordaitean ray pitting has not been investigated along the lines followed out in the Araucarineæ, but I have observed that in *Dadoxylon Brandlingii* (McGill Collection) there is a retention of the scalariform ray pitting in the medullary regions after the ordinary adult pitting has been established. The sections were not, however, sufficiently radial for me to follow the sequence of changes.

#### b. *The Torus.*

In the Gymnosperms the mode of development of the bordered pit and the presence or absence of a limiting membrane in it were questions to which much attention was given by anatomists in the last half of the past century. SANIO (1873),† to whom we owe the discovery of the "torus" in *Pinus*, and the final demonstration of the closed pit in this form, a condition which he thought characterised the whole of the Gymnosperms, has briefly summarised the work of previous investigators (pp. 92-96). His masterly demonstration and statement of the case have, no doubt, been responsible for the fact that until recently all the Gymnosperms have been considered as conforming to this type. In 1907, however, GWYNNE-VAUGHAN, at the Leicester meeting of the British Association, opened the controversy again by his conclusion that there is no limiting membrane in the pitting of certain ferns. In his published account (1908) he states his inability to discover a pit-closing membrane either in the Cycad or the Araucarian material he had at his disposal. Before reading the article by Prof. GWYNNE-VAUGHAN, but instigated by his work, which I thought applied only to the ferns, I examined material of the Cycads in connection with my work on the Araucarians, and came to the same conclusion as he (fig. 39, Plate 4), my independent work thus confirming his opinion in the case of the Cycads.‡

\* This feature was observed and its import noted in the laboratory at Toronto some time before Mr. BAILEY's article was written.

† In speaking of his discovery, he states (p. 78): "Diese scheibenförmige Verdickung der Scheidewand ist bisher übersehen"—a statement which Miss GERRY (1910) has inadvertently taken as referring to the so-called "bars" or "folds" of Sanio, in a recent article on the distribution of these structures in the Conifers.

‡ The writer recognises that GWYNNE-VAUGHAN'S results have been criticised by both BANCROFT (1911) and HALFT (1910). It does not matter, however, so far as the present work is concerned, whether there is an entire absence of the limiting membrane of the pit or only a great reduction of it, and certainly the latter is the case, even if the former should not prove to be so.



With regard to the Araucarians Gwynne-Vaughan's tentative statement holds good with but slight modification. In some material I have found a few pits towards the ends of the tracheids of the autumn wood, where the middle lamella is very thick, with a torus of a peculiar form, spindle-shaped in section and not flat disc-shaped as is characteristic in *Pinus* and related forms. I have not found a torus in the young secondary wood of the root nor in the first year's growth of the stem. It is absent also in the cone axes and in the primary wood of the root. A middle lamella does, however, develop at the cambium, and persists for several tracheids inwards from it, but disappears entirely, I believe, in most cases.

SANIO, in describing the torus in the wood of *Pinus silvestris*, found that the old stem wood was the most useful for his purpose, because of the larger size of the elements, and practically confined his demonstration to such wood. I have examined the primary wood of the root and, as well, the young secondary wood of the stem, root, cone axes and seedling of *Pinus strobus* and *Pinus resinosa*, and have found a torus well developed in all these regions. It is present in the other members of the Abietinæ as well as in *Pinus*. In the Taxodineæ and Cupressineæ it is also a clearly defined and well-developed structure. Even in the Pityoxyla from the Cretaceous the torus has been preserved (fig. 42, Plate 4), as is the case also in *Araucariopitys*.

On the other hand, in the primary wood of *Saxegothaea* and as well in the secondary spring wood of the root, there is scarcely a trace, if any, of a torus; but in the stem, especially in the autumn wood, in the pits of both the radial and tangential walls, there is very often a closing membrane stretching across the pit. In the young branch of *Microcachrys*, all the material of this form which I had at my disposal, I have not found a trace of the torus. In *Dacrydium* there is a closing membrane in the pits which is not very clearly defined, but, if anything, more evident than that in the stem of *Saxegothaea*. In both forms there is a very small thicker spot in the very centre of this membrane. In *Podocarpus* stem the torus is a very definite structure, more like that of the pines in form, being flattened disc-shaped in old wood of *P. Totara* and lens-shaped in *P. polystachya*. In some young root wood of *P. Mackoyi* I have found the torus in about the same stage of development as in *Saxegothaea* stem. It is very much smaller in proportion to the size of the pit, however, than in the pines and their allies, not extending, or but slightly, beyond the opening of the pit. Of the Taxineæ I have only examined old stem wood of *Taxus brevifolia*, and here there is only a poorly developed torus, which so far as I could determine was not more fully developed than in *Saxegothaea*.

From the above described features of the distribution and character of the torus in the Araucarineæ and Podocarpineæ, these groups are seen to form a progressive series, a torus having been gradually acquired in the higher forms. That of *Podocarpus*, while resembling that of the pines, is thus phylogenetically distinct from it, the torus in the *Podocarpineæ*, like the winging of the pollen grains in the



same group, as the writer has shown (1909, *a*), having been acquired independently of that in the Abietinæ.

I have examined very carefully the beautiful sections of *Cordaite Brandlingii* (McGill Collection) from material obtained from St. Etienne, and though the details of structure are even better preserved than in the Pityoxylon forms, I have not found the slightest trace of a torus. I have also examined sections of many other less well-preserved Cordaitean forms, with a similar result. It would thus seem reasonable to consider that the torus is absent, a feature which one might expect in the Cordaiteæ as a whole, a group which is recognised to-day as anatomically very intimately associated with the Pteridosperms, and through them with the ferns themselves, in the modern forms of which no torus is present, and in some cases, at least, no pit closing membrane.

At one time it seemed that the absence of a torus might be accounted for physiologically, and the size of the leaf suggested itself as the factor in question. The similar state of development, however, alike in the large-leaved and small-leaved Araucarias, makes it impossible to account for the absence of a torus on this basis.

The lower Gymnosperms, the Cycads and Ginkgo, stand in intimate association with the Araucarians in so far as the lack of a torus is concerned. On the other hand, in the Gnetales generally, a torus is as typically developed both on the tracheæ and the tracheids as it is in the pine alliance (Abietinæ, Taxodineæ, and Cupressinæ). THOMPSON (1912 *b*) has shown that in Ephedra it is by the degeneration of the torus of the large pits that the "vessels" are formed. He finds, however, that some of the ordinary pits are Araucarian and infers an Araucarian-Abietinean ancestry for this genus. It will be interesting to know which pitting is of the ancestral type, a feature which can be cleared up by a regional study of the individual forms. In a preliminary investigation of the lower Angiosperms I have found no torus present in the multi-seriate pitting of the tracheæ or tracheids. These forms are thus to be associated with the Araucarians, Cycads, Ginkgo, and the ferns in this feature. It will be interesting to find whether a torus is present in any of the lower Angiosperms in connection with the evolution of their vessels. An intimate study of the point will give valuable data on the ancestry of this phylum.

#### c. *Bars of Sanio.*

The "bars" or "folds" of Sanio constitute the "Umriss des Primordialtütpfels."\* SANIO's description is based on a study of *Pinus sylvestris*. He states that it is usually above and below the adult pit, in radial sections, that this border is evident, though in some instances it extends almost completely around the pit. It is part of the primary wall, and is composed of cellulose. From SANIO's description it is clear that he recognised that in young stem wood the "Umriss" came into close contact

\* SANIO, 1872, p. 79.

with the edge of the bordered pit, while in old wood it was considerably removed, forming above and below the pit a "bogenförmige Linie." The primordial pit may enclose two adult pits in stem wood and even more in root wood (p. 79).

This is all the information on the character of the bars of Sanio in the different regions of the individual plant that I have been able to find. Miss GERRY's article (1910) referred to in Section 4b deals with the occurrence of the bars of Sanio in the different groups of the Conifers, but does not attempt a regional study of an individual to gain the phylogenetic evidence from this source. I have examined the cone axis, root and stem wood of the adult and seedling of various forms of the Abietineæ, etc., and find that the thickening of the primary wall described by SANIO is always found in the primitive regions of the plant in intimate association with the pit. It is very small in these regions as compared with its condition in later root and stem wood. In fact, where the pits are multi-seriate, as in young root wood, there may not be a trace of the bar of Sanio (fig. 36a, Plate 4). In a stage toward the adult condition these bars connect horizontally, extending beyond the pits themselves and connecting between the series of pits by mere traces at first (fig. 36c, Plate 4), which later become as thick or even thicker than the original parts. Finally, the bars may become quite separated from the pits, as is the typical condition for the adult wood. It is thus seen that the bar of Sanio is a very much smaller structure in the early formed wood, and that in addition it is closely related to the pits. In Pityoxylon of the Cretaceous the bar of Sanio occurs in contact with the pits also and scarcely extends beyond them (fig. 42, Plate 4). It is quite comparable in this respect to that occurring in the cone and the young root and stem of the Abietineæ of to-day. That the bar of Sanio was relatively small and closely associated with the pits in its primary form is thus sufficiently evident.

When one turns to the Araucarians for the homologue of the bar of Sanio, one is at once struck with the keenness of GOTHAN's criticism of Miss GERRY's result. He thinks it perfectly natural that there should not be a bar of Sanio in these forms, since there is no room for it.\* There is certainly no room for a large one, but I consider that a rudimentary bar of Sanio is present in all the Araucarineæ. The small dark areas which are so common above and below the pits (fig. 37, Plate 4), especially when these margins are free from other pits, are certainly of the same composition as the bars in the Abietineæ. To demonstrate their character beyond a doubt I examined very carefully the tangential section, and found that where the pits separate slightly there is a thin cellulose bar in contact with each pit.

In studying the bar of Sanio to try to determine its origin I was struck with what on first sight appeared to be a well developed bar of Sanio in connection with the transitional pitting. When a series of pits is developed on one of the openings between the scalariform bars, very often none develops on the one above and below and slits remain between the series of pits (fig. 31, Plate 4, see the second tracheid to

\* GOTHAN, 1910, p. 32.

the right). These later fill with a dark cellulose-staining substance. This may be the beginning of the bar of Sanio, but at present the evidence that it is so is insufficient. Work is also being done along the line of the relationship of the bar to the size of the pitting. The bar is certainly best developed in those forms in which the pits are large. The pitting and bar in the Araucarinæ is the smallest of that in any of the Conifers. In *Saxegothæ* there is an interesting condition: there is a poorly developed bar of Sanio which in young stem and root wood is quite Araucarian in character, as is the pitting itself in these parts, two- or three-seriate, and sometimes even flattened by contact. The pits do not increase very rapidly in size and the primitive form of the bar of Sanio is retained for some distance from the primary wood. Another peculiar feature is the even more accentuated Araucarian character of the bar of Sanio in some wounded stem woods of this form. Further investigations are being made along different lines, but sufficient evidence has been put forward above to show that the Araucarians are not to be separated from the other Conifers because of the lack of a bar of Sanio, but rather that they are to be regarded as the basic forms from which this structure in the other Conifers has been derived.

#### 5. RESIN TISSUE.

PENHALLOW (1907), in his work on the anatomy of the Gymnosperms, considers the material deposited in the tracheids adjacent to the medullary rays in the Araucarinæ as resin, and distinguishes the elements in which it occurs as "resinous tracheids." He considers that they have lost their function as conducting channels and compares them physiologically (p. 57) to the tylosed tracheæ of the Angiosperms, regarding the obstruction to vertical flow as further indicated by the usually greater thickness of the wall of the tracheid where the resin is deposited. He distinguished the usual forms of the deposit of resin in the tracheids from bands of Sanio, and from unpitted transverse walls and took pains to determine whether it is really resin or not. The conclusion that the deposit is resin was arrived at after considerable difficulty in getting it to give the proper chemical reactions and colour stains. His difficulties have been fully appreciated in the present work, for, apart from there being great differences in the physical condition of resin there are very many chemically different resins. There are also few good microchemical tests for any kind of resin.

Mr. W. A. McCUBBIN kindly undertook to look into the chemical side of the resin question, and it is from his results that the following statement is taken: "Resin plates (in the tracheids) contain a substance which colour and appearance indicate to be resin, but which is not soluble as are the free resins. This insolubility, however, is shared with undoubted resins in other cells. Its inability to take up alkanna is also not peculiar to itself but occurs in resins in other places. On treatment with Eau de Javelle globules are formed which take up alkanna, and in this the other unstainable resins behave similarly. The amount of resin in the plates seems to be very variable, but is not usually very large, the greater part of it remaining after the resin

has been taken out. This portion, as is shown by the colour reactions, probably consists of a mixture of cellulose and pectose mucilage." Though the plates are not really resin, or even largely composed of resin, for convenience PENHALLOW's designation will be followed. From the standpoint, however, of the writer's view of the origin of resin tissue in the Conifers the fact that the plates are largely composed of cellulose-pectose compounds is as important as the fact that they contain resin.

With regard to the development of the resin plates PENHALLOW (p. 56) states that "the resin gathers locally upon the inner face of the tracheid wall, and as its volume increases it projects from all sides towards the centre, where it coalesces to form a continuous and imperforate septum." The form of the resin deposit that I have found is not such as can be accounted for as above. It does often appear in radial and tangential sections (fig. 41, Plate 4, and figs. 44*a* and *b*, and 47, Plate 5) like plates or spools, but with proper stain it may be seen to line the tracheids far above and below the transverse part. In fact where two spools come fairly near one another in vertical sequence, the ends of the spools unite. When similar appearances are found in both sections this can only mean that the deposit encloses a cavity. Smaller bubble-like cavities may also occur in the axis of the spool or in the body of the deposit itself when this is large (figs. 44*a*, 47, 50, and 52, Plate 5). There seems only one conclusion possible from this, that the form of the deposit is due to a drying-out process or to surface tension between non-miscible fluids. Perfectly similar deposits were formed artificially in sections by both means. The plate itself when carefully examined nearly always reveals traces of its "double meniscus" character (figs. 44*b* and 47, Plate 5. See also the *Dadoxylon* section, fig. 46).

The association of this deposit with the medullary rays (figs. 44*a* and 47, Plate 5) makes one suspect that the ray cells are the source of the material, and this especially since resinous material is found in the ray cells and often in similarly shaped deposits (fig. 44*a*). There is another source, however, the residue of the protoplasm in the tracheid itself. That there is a concentration of the tracheid plasm at the medullary ray is indicated by the greater thickness of the wall at this part (fig. 44*b*). Naturally, too, this would be the "last stand" of the protoplasm of the tracheid because of its dependence on the ray cells for supplies. That the resin is deposited, too, while the tracheid has still fluid contents is evident from the form of the deposit itself. The deposit thus appears early in the tracheid and probably contains some of its protoplasmic contents.

The amount of the deposit in the tracheids varies very much in different species. The greatest amount that I have observed in a living form was in *Agathis bornensis* (figs. 40, Plate 4, 50 and 52, Plate 5). The deposit, too, is found in certain fossil forms. In *Dadoxylon materiarium* (fig. 43, Plate 5) it shows clearly in the tracheids along the medullary rays. In *D. Brandlingii* it is very abundant (fig. 46,

Plate 5, to the right), and in this species shows its meniscus formation very clearly. These two forms are preserved as petrifications, but in a species of *Araucarioxylon* from the Cretaceous whose tissues themselves are present, resinous tracheids are very abundant along the rays (fig. 45, Plate 5). In radial section the form of the deposit in this fossil is quite similar to that in *Agathis australis* (compare, for example, figs. 44*a* and *b*, and 48*a* and *b*, Plate 5). The deposit is more often clearly marked in the summer wood of the annual ring (fig. 57, Plate 6) and undergoes a tangential extension in this region.

PENHALLOW considered that the resin deposits in the tracheids might be mistaken for bars of Sanio or for cross walls in tracheids. I have had more difficulty in distinguishing them from the trabeculæ which are so common in the Araucarinæ, and apparently in other Conifers as well. These trabeculæ often are so spool-shaped in radial sections that when unstained they simulate very closely the resin. They also occur in association with the rays. When double stained for cellulose and lignin, however, they give very definite evidence that they are of exactly the same composition as the wall of the tracheid. They have even a small rod of the middle lamella enclosed by ligneous material. This central cord connects with the middle lamella of the tracheid at either side. The trabeculæ are thus laid down in the very young tracheid before the secondary wall is begun. These trabeculæ are *partial* septations of the tracheids and seem like abortive attempts at the formation of septate tracheids.

The complete septation is also fairly common in the Araucarinæ. It occurs mostly on the outer face of the summer wood (fig. 49, Plate 5), and I have found it more frequent in *Agathis bornensis* and in *A. alba* than in any other forms. The former has a great amount of resin deposit in its tracheids (fig. 40, Plate 4, and fig. 52, Plate 5), and the latter is the source of the dammar of commerce. The septa have unusually numerous bordered pits, and when seen in transverse sections the pits appear closely packed, and practically fill the tracheid.

In connection with the septate tracheids there are often parenchyma cells replacing some of the septated parts. This may go so far that the whole tracheid is replaced by parenchyma, but usually there is some vestige of the origin of these vertical series of cells from the tracheary elements. Often the end segment is abnormally thickened (fig. 50, Plate 5 at *a*), a sclerotic cell with fine pores which expand towards the primary wall, and retain this indication of their derivation from the bordered pit of the ordinary tracheid. Their walls show concentric layering as clearly as is the case in other sclerotic cells. They are probably to be regarded as by-products in the process of parenchyma formation from tracheary tissue. The length of the parenchyma cells which are formed in this way is very variable. In some instances I was unable to discover any septum for the whole length of the adjacent tracheids in the same radial row with it. The parenchyma derived from the tracheary tissue has been found in many species of *Agathis*, in both stem and root



wood. In the root the parenchyma often occurs in the young wood where a single row of tracheids divides to form two. In fig. 51, Plate 5, the third element in the upper row after the dichotomy of the single row is a parenchyma cell. These parenchyma cells are frequently associated with the beginning of a medullary ray, but I have not definitely determined their relationship to ray formation, though it would appear that a single vertical series of parenchyma cells originates several rays. Often, too, vertical divisions, both radial and tangential, occur in the parenchyma cells, and a mass results from the originally single cell. I have observed this only in the root.

After satisfying myself of the presence of parenchyma in the secondary wood of the Araucarinæ, and of its derivation from the tracheary tissue, I found that as long ago as 1862 SCHACHT had come to very nearly the same conclusion when studying the wood of *Araucaria brasiliensis*. After describing the cells which he criticises GOEPPERT for considering resinous, he says that they are to be regarded as "abnormally developed wood cells." Had the technique of the day been good enough SCHACHT would undoubtedly have found the transitional stages between tracheid and parenchyma and been able to determine that these elements were in vertical series which replace certain tracheids of a radial row, that is, that they are developed from the same cambial cell which ordinarily gives rise to tracheids, and are therefore potentially tracheary. When one considers that the ancestral Palæozoic woods were characteristically devoid of parenchyma,\* it is impossible to consider that the parenchyma could have originated in any other way.

In the Podocarp line the resin tissue takes the form of resinous tracheids and parenchyma cells. The latter are found normally in series which are coterminous with the tracheids which they replace in radial sequence, and are thus ancestrally tracheary as in the Araucarinæ.

In *Abies* and *Sequoia*, PENHALLOW (1907) found in his study of the resin cysts short, parenchyma-shaped, tracheary elements continuous with parenchyma in the vertical direction, and even discovered transitions between the two types of elements. These features he interpreted as an indication of the origin of one type of element from the other, but recognised that the sequence might be read in either direction. He decided, however, in favour of the derivation of the tracheary structures from the parenchymatous, and designated the former on this account *parenchyma* tracheids. One of his chief reasons for so deciding was what he considered the homologous process in the formation of ray tracheids from parenchyma. THOMPSON (1910) has since shown, however, that the ray tracheids are not derivatives of parenchyma, but that they originate as short vertical tracheids, and later extend along the medullary rays, and that whatever of transformation occurs, is in the inverse direction—a formation of parenchyma from the tracheary elements. The significance of PENHALLOW's comparison is thus reversed, and any weight which it had must now

\* There are exceptions to this, as GOTHAN (1910) has pointed out.



favour the tracheary origin of the parenchyma of the resin tissue. Moreover, in *Abies* the septate tracheids and parenchyma cells are in vertical series which replace tracheids. They are thus derivatives of a cambium cell which ordinarily gives rise to a tracheid, and as such are of tracheary origin. I have found in *Abies* that the septate tracheids and parenchyma cells are in vertical series which replace tracheids. In the pines, too, this is true of the origin of the tissue surrounding the resin canals, although there is a difference between the mode of formation in the two genera—a difference which is important and will receive attention in a future publication. In the pines and *Abies*, then, the ligneous resin tissue owes its origin to a replacement of tracheids by various elements: resinous tracheids, septate tracheids either resinous or non-resinous, and parenchyma. These are usually aggregated around the so-called resin canals, but I have also found resin tracheids in the root of *Pinus* and in the seedling and cone axes of this genus, not connected with the resin canals. They show the same morphological and chemical forms of the deposit in these regions as in the *Araucarinææ*, and I consider their presence here a retention of the primitive condition which is found in the *Araucarinææ* and the *Cordaiteæ*.

The vertical resin canals of the pine alliance are in intimate association with the medullary rays, these canals forming an anastomosing system with those which occur in the latter. Their intimate association with the rays is a very natural one when it is considered that the ray is the source of the preservative in the ancestral forms which are devoid of ligneous resin tissue in their secondary wood. This is indicated also by the close association of the resinous tracheids with the medullary ray in the *Araucarinææ* and *Cordaiteæ* and by the fact that when a parenchyma cell replaces all or a portion of a septated tracheid the parenchyma is always in very intimate association with vertical series of medullary rays, a feature which is very noticeable in studying tangential sections. KIRSCH (1911) has recently propounded an ingenious theory to explain the intimate association between the parenchyma of the ligneous resin tissue and that of the medullary rays. He studied the pines chiefly, and considers that the tissue of the vertical resin canals has been proliferated from that of the rays. There is no doubt that the ray has had a great modifying influence on the production of the vertical resin tissue, and perhaps even in the most highly organised forms it does give of its cells to the building up of this tissue. It is not conceivable, however, that in the *Cupressinææ*, for instance, the vertical series of the resin cells replacing a tracheid could have been proliferated from different uniseriate medullary rays and been so concentrated on one tracheary element as to wholly obliterate and completely replace it. Nor can one see why there should be septate tracheids surrounding the parenchymatous tissue of the vertical resin canals if these septate tracheids are not in the nature of transition stages between tracheids and parenchyma cells.

The origin of the resin tissue of the pine alliance from tracheary elements as in the *Araucarinææ*, and the retention of similar stages in its development, forms what the

writer regards as one of the fundamental features of relationship between these two groups. The rays of the pines have undergone much specialisation, however, as has the ligneous resin tissue itself—the formation of resin canals. This is a difference, however, which merely indicates the higher state of development of the resin tissues and has no doubt been derived from the aggregation of the resin cells and the degeneration of certain of the central ones, a feature which PENHALLOW (1907) has already emphasised. That this has been the course of events in the pines is indicated by the fact that the canals form at the cambium as solid masses of parenchyma and that the traumatic canals of the pines are usually solid (figs. 61, 62, and 65, Plate 7). Very often, too, this is their character in the cone axis (fig. 64, Plate 7). Again there are many references to the so-called tylosed condition in the fossil forms, but until it has been proven that these canals were ever open they must be considered as originating and remaining solid. Even in the living forms the true tylosed condition is very much less usual than ordinarily thought, as some work which Mr. C. H. MORSE is carrying out shows. It is not to be inferred that the writer considers there are no open resin canals in the Conifers, but only that the solid form is ancestral and that this is indicated ontogenetically, traumatically and from the ancestral forms themselves.

#### 6. MEDULLARY RAYS.

The medullary rays of the Araucarineæ consist typically of thin-walled parenchyma cells. At the pith these are elongated vertically like the neighbouring cells of the medulla, while in the old wood their long axis is in the radial direction. This difference in the medullary ray cells is found in other Conifers also,\* but in no other forms does it appear so marked as in the Araucarineæ, and especially in the root of these. The elongated cells are at first of more or less regular form, but shortly after entering the secondary wood they develop a pair of opposite horizontal processes which make these cells appear four-armed in radial section, with large intercellular spaces. The horizontal arms elongate at the expense of the vertical ones and organise several distinct rays, usually one to two cells high. In old wood the rays are considerably higher. To find out definitely what happens to the rays as they pass outwards from the pith and how new rays originate, series of sections of wood of both root and stem about 20 years of age were prepared. These were made just a little off the radial so that the rays could be followed the more easily. By cutting them about  $15\mu$  thick the extent of the rays in each was about as great as the year's growth, so that 15 or 20 sections had to be examined to trace the rays from the pith to the cambium. Of 70 stem rays of *Araucaria imbricata*, 20 retained the same number of cells throughout their course. Most of these were two cells high, but one was four. Thirteen increased by the addition of one or two rows. Nine decreased similarly from the pith outwards. Two increased, then decreased to the original number again. There were also quite numerous cases of

\* KNY, 1884, p. 219, fig. 7.

fusion of rays, some of separation, and also perhaps more with fusion, separation, and re-fusion. In the root similar conditions were observed. In the root and stem the rays are higher in the old wood, the root rays being higher than those in the stem. The root rays differ from the stem also in their more numerous irregularly elongated or four-armed cells from which the new rays originate (fig. 28, Plate 3). New rays almost invariably come from such cells which are in connection with other rays. These elongated cells form a striking feature of the root wood in radial sections. SCHACHT noticed them as long ago as 1862 in *Araucaria brasiliensis*, but did not observe their relationship to the formation of rays, nor did he find any trace of them in the stem. They occur in the cone axis as well as the root, and most rays originate in the secondary wood of the root from them even far from the pith. In the stem the elongated elements seem to be pretty well confined to the circum-medullary region. Similar conditions to the above were observed in stem and root wood of *Agathis* (*A. bornensis* and *A. Moorei*). SEWARD (1906, p. 344) has compared these irregular elongated cells to those of *Sphenophyllum plurifoliatum* described by WILLIAMSON and SCOTT (1894, p. 924). This feature is probably an ancient one in both instances, indicative of the organisation of the medullary rays from vertically elongated elements. The ray tracheids of the higher forms came from such elongated tracheary elements, not at the pith but farther out in the secondary wood, and had to "learn" to grow in the radial direction. The ray tracheids leave a "tail" behind them in this process,\* but the only indication left by parenchyma cells of the rays is their oblique and irregular end walls, and the chinks which occur among them.

I found a curious feature in the branch of *Agathis australis*, which shows how closely related the medullary ray cells near the pith are to the pith cells themselves. In the Kauri the pith of the branch is almost entirely composed of irregular sclerenchyma cells. These in the region of the exit of the leaf trace from the stem cylinder are found at first completely forming the rays. Farther out they get fewer, and at about the middle of the first year's growth completely disappear, and are replaced by the normal thin-walled cells of the ray (fig. 53, Plate 6). At first I thought it possible that these thick-walled ray cells, coming as they do in the first year's wood, might be a vestige of the thick-walled condition which is characteristic of some of the Abietinæ. The great thickness of the wall, however, and their evident sclerotic character made me abandon this idea, especially when I found similar small, simple and branched pits on these ray cells, as are present on the sclerotic cells of the pith (fig. 54, Plate 6). My conviction was confirmed when it was observed that they do not occur in the seedling nor in the axis of the micro- and mega-sporangiate cones. In the seed cone axis the sclerenchyma is in "nests" as in *Lyginodendron*,† and as in the latter the medullary sclerotic "nests" pass

\* THOMPSON, 1910.

† See SCOTT, 'Studies,' fig. 129.

through the broad leaf gaps, so in the former they accompany the cone scale trace in its outward course. It is readily conceivable that a similar process is going on in the *Agathis australis* stem, but that, the woody cylinder being more compact, these sclerotic elements become embedded in the ordinary medullary rays near the leaf trace. I have found a few similar cells in other species, but nothing to be compared with the conditions in the Kauri.

The medullary ray cells are then characteristically thin-walled in the Araucarians, and are comparable to those in the Cordaitean forms. They are also unpitted in the Araucarineæ as in the latter. Often these cells have been wrongly spoken of as having pits on the lateral walls where they come into contact with the tracheids, some anatomists even going so far as to distinguish the pitting as of the bordered type. GOTHAN has noted this especially in the case of PENHALLOW (1900), when discussing the latter's statement that there are ray tracheids in *Cordaitea Clarkii*. He says that all PENHALLOW's ray cells are tracheids on account of their pitting. With this as a basis and the fact that the ray tracheids have not been figured, he goes so far as to question this unique example of their occurrence in the Cordaitean forms. I have examined carefully the type set of sections and have found no evidence to contradict GOTHAN's conclusion.

The Cordaitean and Araucarian forms thus agree in the parenchymatous and unpitted character of the ray cells. The cells of the former, too, are long in the pith region, as I have observed in the type form, *Dadoxylon Brandlingii*. This, too, must be characteristic for the Cordaitean forms, for GRAND' EURY (1877, p. 262) speaks of the ray cells, in general, as being nearly as high as long. I take it, however, that his statement must apply to young wood especially, for the numerous specimens in the McGill University collection which I have examined do not show this to be characteristic of the old wood.

Since these two groups have medullary rays composed wholly of parenchyma, the question arises as to the means they adopt for the radial conduction which is carried on by the ray tracheids of the forms which have developed these structures. The tracheids in adjacent radial rows are frequently alternate with one another, and since they have their pits in several series on the radial wall (especially at the ends of the tracheids) the water can by a zig-zag course make its way in the radial direction. The more or less polygonal and irregular form of the tracheids no doubt facilitates this transfer. In fig. 55, Plate 6, beginning at *a*, water could pass radially through eight tracheids. When a thin (about  $7\mu$ ) transverse section shows so many tracheids in radial communication, this must be quite a perfect system for radial conduction. In addition, the tracheids very often in the Araucarian forms have ends bent horizontally which touch the rays above and below, or at the side. WINKLER (1872, Plate 7, fig. 1) has figured such tracheids in *Araucaria brasiliensis*, and I have found them quite common in all the forms that I have examined. They appear much more readily in macerated preparations than in sections. I cannot say that

they are common in the Cordaitean forms, though I have found them in a good many instances. Similar structures replace true ray tracheids in the pine cone as shown by THOMPSON (1910), and since the ray tracheids originate from short tracheids which "bend along the ray," he suggested that we have in these tracheids with bent ends the precursors of the true ray tracheids.

Ray tracheids are specialised structures, as they occur in the pines and their allies to-day, as indicated not only by their mode of development, but by their absence from the cone and from the first few years of stem and root wood. In the fossil Abietinean forms, too, they are not abundant, and have only been recorded in old wood. The ray tracheid is a structure which is considered by JEFFREY to have made the pines the dominant group of the Conifers to-day,\* one which if ever acquired would certainly seem to be too advantageous to be readily lost. If the Araucarineæ are derived from the Abietineæ, the absence of ray tracheids can be accounted for by either of two views; that they came off from the Abietineæ before these had acquired ray tracheids, or that they once had them in their ancestry and have lost them. Their absence may thus be either palingenetic or cenogenetic. The oldest form with ray tracheids is from the Cretaceous, and since the first Araucarian appeared long before this, the absence of ray tracheids in the Araucarineæ must be palingenetic. When the thin and unpitted character of the walls of the ray cells is also taken into account, it is evident that the ray cells are of primitive type. In fact they are identical with the Cordaitean and much more primitive than those of the Abietineæ.

#### 7. BAST AND PERIDERM.

The bast in *Agathis* and *Araucaria*, according to STRASBURGER (1891, III), has no albuminous cells associated with the rays. These he considers as the counterparts in the bast of the ray tracheids in the wood, and finds that in exceptional cases only are they not continuous with ray tracheids. Some of these cases have been explained by the fact that the ray tracheids which were ancestrally present have been lost.† The absence of the marginal medullary ray cells from the bast of the Araucarineæ (and Taxineæ), STRASBURGER (1891; III, pp. 92-93) considers evidence of their primitive structure. It is certainly almost in the nature of a demonstration that these forms have had no connection with the Abietineæ after the latter had developed ray tracheids and albuminous marginal medullary ray cells. A study of the bast of the Conifers is perhaps more urgently needed at present than that of any other feature. I have found no albuminous cells in *Podocarps* which I have examined, and it would seem as if this might be another feature which divides the Abietineous alliance of the Conifers from the Araucarian. (See Section 4a.)

Periderm is of relatively late development in the Araucarian stem. In the root it

\* JEFFREY and CHRYSLER, 1906, p. 14.

† THOMPSON, 1910.



appears comparatively early, as in some, at least, of the Abietineæ, where it comes in with or before the secondary wood. Its tardy development in the stem may be in association with the foliage habit, and it will be interesting to determine its relationship to the primitively persistent foliage of the Araucarineæ, the leaf bases in some forms of which remain on the stem for many years, and, as was stated before, form an "armour" quite comparable to that of the Cycads.

#### 8. ANNUAL RING AND TANGENTIAL PITTING.

The presence or absence of annual rings in the Araucarineæ has been a matter of much dispute. This has resulted from individual variation and possibly also from the fact that in some forms the rings are clearly marked, while in others there is a ringed appearance to the naked eye, which on examination with the microscope in transverse section is not evident. It was this which led SCHACHT (1862) to state that there are *no* (his own italics) annual rings in *Araucaria brasiliensis*, but only an appearance of concentric circles. He says, further, that the circles are incomplete and that in the radial direction also the rings "are lost gradually either on both sides or on one side, and frequently, indeed, this is the outer side, whereas in true annual rings, at least in the stem, the transition from spring to summer wood is the more gradual." The trunk material which SCHACHT examined came from Brazil. WINKLER (1872) confirms the absence of annual rings in greenhouse material of the same species; the tree was *thirty* years old but showed only *eighteen* rings. He does not, however, agree with SCHACHT as to the rings themselves, but considers that they show very good alternations of smaller thicker-walled cells and larger thinner-walled ones, "if the 'elegant' distinction between spring and autumn wood in *Pinus sylvestris* be left out of consideration." STRASBURGER (1891, III) has referred to the annual ring both in *Agathis* and *Araucaria*. He agrees with SCHACHT that the ring is poorly developed in *A. brasiliensis* (p. 85), that is, that there is but little differentiation in size between the autumn and spring tracheids, but refers to another feature to which he attaches importance, the presence of tangential pitting on the last and possibly also the second last element of the summer wood. WINKLER (1872, fig. 2, Plate 7) had already figured tangential pitting in this species, though he does not seem to have recognised its relationship to the annual ring. Of *Agathis australis*, STRASBURGER (p. 38) says the annual rings are clear, but does not refer to the tangential pitting. In PENHALLOW's work on the North American Gymnosperms a chapter is devoted to the growth ring, and in it he refers to the annual ring of *Araucaria* as "not determinable, or, at most, poorly defined" (p. 28), and to that of *Agathis* as "more or less clearly defined." While in a general way this statement is correct, in that *Araucaria* has possibly a less clearly marked growth ring than its sister genus, it is inaccurate in that distinct growth rings do occur in *Araucaria*. DE BARY (1884, p. 513) states that he found annual rings in *A. excelsa* "sharply marked when seen with the naked eye, and confirmed their presence with

the microscope." SEWARD and FORD (1906, p. 339, Plate 24, fig. 17c) found and figured clear annual rings in old stem wood of *Araucaria imbricata* grown at Kew, but notes that this is not "satisfactory proof of their occurrence in Chilian trees." The annual ring in *Araucaria Cunninghamii* in BAKER and SMITH's 'Pines of Australia' (fig. 237) shows a very definite boundary between the spring and summer growth in old wood of this species. In *Agathis robusta* the same authors have also figured (fig. 262) a clear annual ring, though SEWARD and FORD (1906) state that "in *A. robusta* the rings are either absent or very faintly marked" (p. 341). In this species of *Agathis* and in several others of both *Agathis* and *Araucaria* I have found clear growth rings (e.g. see fig. 40, Plate 4).

Whether they are *annual* rings or not, has not been determined. Often the ring may be very much of the type described by SCHACHT, and in the Araucarinæ we have all stages between a clear demarcation of the season's growth and one in which there is no definite boundary determinable, but in which the elements of the spring and summer wood pass so insensibly into one another in both directions that it is impossible to tell which is the outside, and which the inside of the stem. Growth rings of the root type are also present near the pith. They may have only a single row of summer elements with the adjacent elements on the inner and outer sides almost equal in size (fig. 60, Plate 6). What may be called "inverse" rings are also met with (fig. 59, Plate 6). Tangential pitting on the "summer" elements of the upper ("inverse") growth ring makes its character the more misleading. Just such indeterminable growth rings characterise the Paleozoic forms. Even in the Triassic GOTHAN (1910, p. 8) says that clearly defined growth rings are only exceptionally present.

In Cordaites the indications of growth rings that I have observed are of the same type as the indeterminate ones of the Araucarinæ. The most clearly marked that I found was in a *root* (fig. 56, Plate 6) from the British Coal Measures. In an *Araucarioxylon* species from the Cretaceous I have also found some poorly marked growth rings (fig. 57, Plate 6) which seem to be of very irregular occurrence. In the sporadic character of the growth ring in the Araucarinæ there is thus a combination of the features of the ancient forms and of the present day Conifers.\* That the growth rings in the Araucarinæ are in the process of acquirement seems to be the natural inference from the observed facts.

The occurrence of tangential pitting on the summer wood of the annual ring is stated by STRASBURGER to characterise all Conifers which lack ray tracheids in their medullary rays. The inverse statement has exceptions, in certain hard pines, where STRASBURGER considers that the ray tracheids are so well developed that they have replaced it functionally.† That the tangential pitting has originated in the Araucarinæ in connection with the development of the growth rings is indicated by some preliminary work that I have done, but further work is needed to establish this

\* Cf. PENHALLOW, 1907, p. 29.

† STRASBURGER, 1891, III, p. 9.

point. The pitting is certainly of a primitive type, the pits usually approximate, often flattened, and alternately bi-seriate (fig. 49, Plate 5, and fig. 58, Plate 6). The pit-pore, too, is oblong, a feature which is considered to have been retained from the scalariform condition (see Section 4a).

In these respects the tangential pitting resembles that of *Pitya antiqua*, described by SCOTT (1902, p. 352, fig. 20, Plate 6), where, however, the pitting is multiseriate. The tangential pitting in the Araucarineae may also be of the so-called "scattered type" (cf. SEWARD and FORD, 1906), though the pits are usually biseriate in this case, occurring in two alternating rows.

PENHALLOW (1907, p. 65) accounts for the occurrence of tangential pits on the summer wood of the Conifers "because of limitations of the radial walls through radial compression" at the annual ring. Evidently if this view accounts satisfactorily for their presence it will not also account for their absence in the hard pines where the rings are well developed. JEFFREY and CHRYSLER (1906, pp. 6 and 7) in their publication on the Pityoxyla of the Cretaceous consider that since "tangential autumnal pits, such as are ordinarily absent in the wood of hard pines, are generally present in their cones," and also in certain fossil forms (Pityoxylon and *Pinus succinifera*), this is an ancestral feature of the pine alliance. The hard pines are the forms with the most numerous and specialised ray tracheids, and it is possible that radial conduction is sufficiently provided for by these elements, as STRASBURGER has indicated, and that the tangential pitting of the summer wood has been abandoned on this account. It will be interesting to trace the gradual development of this pitting, as indicated in the Araucarians, in the early fossil forms for verification of its acquirement in connection with the annual ring, and then after it has been developed to follow the stages of its degeneration in association with the differentiation of ray tracheids. This loss of tangential pitting must have occurred subsequent to the time of the amber formation, in which *Pinus succinifera* is found.

#### 9. SOME FOSSIL FORMS, AND THEIR BEARING ON THE RELATIVE ANTIQUITY OF THE ABIETINEÆ AND ARAUCARINEÆ.

Recently, two interesting genera have been described by Prof. JEFFREY, one from the Cretaceous and the other from the Triassic, with features transitional in character between the pines and the Araucarians. "Araucariopitys was characterised by the possession of deciduous (spur) shoots, which apparently persisted for a single year, by the characteristic radial pitting of its tracheids, transitional between true Araucarian pitting and that found in the Abietineæ; by rays differing from the Araucarian type, and approaching the Abietineous type, and by the formation of traumatic resin canals closely resembling those found in the Abietineæ."\* In 1910, *Woodworthia*, from the Triassic of Arizona, was described, with short shoots, which

\* JEFFREY, 1907, p. 443.

are considered to persist probably as long as the axis which bears them, though the subtending leaf trace disappears early. The pitting is described as of the Araucarioxylon type, and at the ends of the tracheids, as in this form and in Agathis and Araucaria. With regard to the medullary rays, it is stated that these have numerous pits on the lateral walls, but none on the terminal and horizontal, and so resemble the living Araucarians and differ from the Araucariopitys, in which the walls of the ray cells are thick and "strongly pitted, as is typically the case in the Abietinæ."\* Nothing is said of traumatic resin canals, and they are thus probably to be regarded as absent from this wood. JEFFREY considers the transitional features of these forms as proof of the derivation of the Araucarinæ from the Abietinæ, but does not refer to the possibility of their interpretation as evidence of affinity between the Cordaitales and the Abietinæ, though the latter are regarded by him as the most primitive of the Conifers, and the former their representatives in the Carboniferous. The balance of evidence with regard to the relative antiquity of the Abietinæ and the Araucarinæ is made to turn on the crucial point of the "traumatic revival" of resin canals in the forms that JEFFREY considers the ancestors of the Araucarinæ.

Dr. GOTHAN, in his recent extensive account of fossil wood from Spitzbergen,† has described several important transitional forms from the Upper Jurassic. The transitional features, however, he interprets in a different way from that which JEFFREY has done in the case of the forms he has described. GOTHAN states that his Protopiceoxylon, Protocedroxylon, Piceoxylon, and Cedroxylon all *retain* Cordaitæan (Araucarian) features in their organisation, and have *acquired* others, which ally them to the modern genera. These transitional forms described by GOTHAN, coming as they do from the circumpolar region, which is recognised as the "birthplace" of the North Temperate Conifers, are deserving of special attention, since they afford interesting data, as GOTHAN points out, on the gradual acquirement of the secondary ligneous resin passages, both horizontal and vertical, of which structures JEFFREY's work up to the present has simply postulated the *ancestral presence*, in spite of the evident difficulty of harmonising this view with the *absence* of such structures from the most primitive seed plants, the Pteridosperms, and from the recognised ancestors of the Conifers, the Cordaitales, as well. Furthermore, it is not apparent why JEFFREY's transitional Cretaceous form, as his description shows, should possess more affinity with the Abietinæ, in radial pitting, in medullary ray structure, and in the presence of traumatic series of resin canals, and why the older Triassic form should have in corresponding features so much better established Araucarian than Abietinean characteristics, if the Abietinæ are the more ancient.

It is important to consider some of these transitional features of Araucariopitys and Woodworthia in more detail. The two types of pitting which JEFFREY has

\* JEFFREY, 1907, p. 438.

† GOTHAN, 1910.

figured are seen to be very different, if one compares his 1907 fig. 12 ( $\times 500$ ) and his 1910 fig. 5 ( $\times 120$ ). That of the more recent form, *Araucariopitys*, is much more Abietinean (uni-seriate and the pits to the right of the figure distant from one another) than that of *Woodworthia* (the pits bi-seriate usually, hexagonal, and approximate), though JEFFREY (1907, pp. 438-439) states that mainly the more Araucarian type of pitting in the former has been chosen for the figure. He further states of the pitting in *Araucariopitys*: "Occasionally a tracheid may be found in longitudinal section of our species, broad enough in the terminal portion to accommodate a double row of pits, in which case the phenomenon of alternation, as well as flattening, may be observed, although bi-seriate pits are sometimes found to be opposite as in the Abietinæ" (p. 439). The only Abietinean feature indicated in this terminal pitting is that the "bi-seriate pits are sometimes found to be opposite." It is to be noted, however, that the Cordaitean features are "alternation as well as flattening."

I have found that in certain Cordaiteæ there is a parallel to the terminal pitting as above described. In some of the more specialised forms, the pits, though much reduced in some parts, consist of several series at the ends (figs. 27*a* and *b*, Plate 3). It is to be noticed also, near the end of one of the tracheids to the left of these figures (at X), that opposite pits occur in this Cordaitean form, an arrangement which may fairly frequently be observed in different species. It would thus seem more reasonable to consider the occasional opposite arrangement of the pits in *Araucariopitys*, which it shares with the Cordaitean forms, as indicating affinity to these rather than as having been acquired a second time from the Abietinæ. The other Cordaitean characteristics ("alternation as well as flattening"—see above) in the terminal pitting of the tracheid in both *Araucariopitys* and *Woodworthia* render this view the more plausible. The character of the terminal pitting of the tracheids in the living *Araucarineæ* affords corroboration. This is of a more primitive type than that on the intermediate parts, being a vestige of the condition found in the cone axis, where the pitting is multi-seriate, and covers the whole radial surface of the tracheid, as is the case in tracheids of the *Pteridosperms* and the more primitive forms of the *Cordaiteales*.<sup>\*</sup> Thus, the characteristics of the terminal pitting of the tracheid in *Araucariopitys* and *Woodworthia*, considered in the light of fossil and living forms, present ancestral features which ally these forms to the *Cordaiteales*, and not to the Abietinæ.

It is to be recalled in this connection that the living Abietinæ, in their primitive regions, show clear indication of Araucarian or Cordaitean pitting; SCHACHT called attention to this long ago (1862). Figs. 36*a*, *b*, and *c*, show the bi-seriate (sometimes tri-seriate) condition in the root of *Larix*. The pits are often flattened by mutual contact, as in the Araucarians. Moreover, the fact that the ray pitting of the pine tracheid is much specialised in the old wood of stem and root, while in the young wood

<sup>\*</sup> See Section 4a, and cf. GOTHAN, 1907, with whose ideas on pitting in general this is in perfect harmony.



of these regions and in the cone axis these "Grosseiporen" gave place to several smaller pits, is not without significance in this connection (see Section 4a). It is further to be noted that in the older form, *Woodworthia*, the ordinary pitting of the tracheids is practically identical with that of certain of the Cordaitales, while in *Araucariopitys* it is very Abietinean, has even a torus, a condition which is the reverse of that which we should expect if the Abietinæ are the more ancient. When considered from all standpoints, the evidence presented by the pitting decidedly favours the greater age and direct Cordaitan connection of the Araucarinæ.

As in pitting, so in medullary ray structure, *Woodworthia* does not differ in any essential feature from the Cordaitales. The ray cells are thin-walled in both, and unpitted on the horizontal and terminal walls as well. *Araucariopitys* has, on the other hand, thick-walled and pitted medullary ray cells, "as is typically the case in the Abietinæ."

Besides the pitting and medullary ray structure being more Cordaitan in the older form reference has been made above to the fact that, according to JEFFREY'S view, the traumatic resin canals should be better developed here also, whereas they are apparently absent (not reported) in *Woodworthia*, but are well developed in *Araucariopitys*. In connection with this feature the writer would call attention to the many evidences of traumatic resin canals in the oldest fossil representatives of the Abietinæ. CONWENTZ (1890) in his monograph on the Amber pines (*Pinus succinifera*) devotes considerable space to it and figures one traumatic series with 13 canals in it. He considers that wounding was much more prevalent in that period than it is to-day. In many of the Pityoxyla of the Cretaceous there are traumatically arranged, though not so extensive, series of resin canals. SEWARD (1896, p. 422), in describing *Pinites Ruffordii* from the English Wealden, says that "the usually large number of resin canals in certain parts of the section may be regarded as an expression of some injury sustained by the tree." GOTHAN speaks of the abundant traumatic canals in *Protopiceoxylon* from the Jurassic; "Der Querschliß . . . zeigt beispielsweise eine kleine Serie oder Häufung von Harzgängen,"\* and gives an illustration of this in Plate 3, fig. 8. This is one of the oldest authentic representatives of the Abietinæ of which the writer is aware, whose wood structure has been described. The important rôle which wounding has played in connection with the production of resin canals in these old Abietinean forms makes one hesitate to accept the view of the Abietinean ancestry of the Araucarinæ, which practically disregards this feature, and emphasises the importance of their "revival" by wounding in such forms as ancestrally had them in the condition in which they appear normally in the pines of to-day. The difficulty of accepting the latter view of traumaticism becomes greater when one finds that in the pines of to-day the number of resin canals in a given area is greatly increased by

\* GOTHAN, 1910, p. 17.

injury.\* Figs. 61 and 62, Plate 7, are from the stem of *Pinus austriaca* which has been twice double wounded, the second time two years after the first. The stem is about 2.5 cm. in diameter and the response extended all the way around it. Fig. 62 is half-way between the last double wounds. In *P. resinosa* it has been observed that the resin canals may be increased to seven or eight times their normal number by injury (fig. 65, Plate 7). The response is greatest above the wound and may apparently extend through several years of vertical growth. It is interesting to note that in a recent Bulletin of the United States Forest Service HERTY (1911) has shown that the resin canals are increased, especially above the wound, in trees that are used for the production of turpentine.

Although the possibility of increasing the number of resin canals in the pine is being realised commercially, its scientific importance has not been recognised. JEFFREY has apparently overlooked this traumatic production for, after speaking of the great drain of carbohydrate material which was demanded for the upkeep of the complex system of resin passages of the ancestral pine forms, he says: "Gradually the more economical tendency arose of forming resin passages in the case of need only. In *Pinus* this tendency is scarcely observable" (1905, p. 26). The response which has been described above is certainly a very striking one, resulting in seven to eight times the normal number calculated per square centimetre. These traumatic resin canals cannot be regarded as of the "revival" type, since this would postulate in the ancestors of the pines an absurdly large normal number of such structures. The only possible conclusion seems to be that they have *originated*, and this in response to injury. That there are also traumatic resin canals of the "revival" type in the Conifers, the writer agrees, has been clearly demonstrated; structures which have originated in connection with wounding, and have been lost, should certainly stand first chance of being revived by the same means. Such series are to be found in *Abies*† and in *Sequoia*‡.

From a study of the living forms it is apparent that these two types of resin canals are distinguishable, but the evidence on this point will become more complete when the ancestors of the Abietinæ are definitely connected with their Cordaitan or Araucarian allies of the Palæozoic. Two points only will be referred to here. By comparing figs. 67 and 68, Plate 7, it will be seen that there is a striking resemblance between the traumatic resin canals of *Araucariopitys* and of the normal ones of the pine cone figured. The resemblance is accentuated by contrast with the traumatic series of such a form as *Abies* (contrast text-figs. 5 and 6) where it has been proved that the resin canals are *revived* by injury. The series of the latter are in much more definite rows, and further all the canals in a series are in close

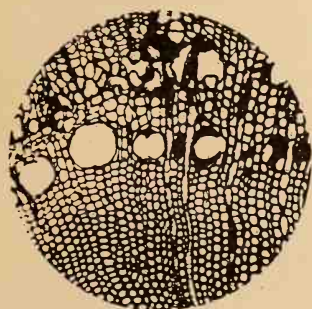
\* Mr. C. H. MORSE is working on this and other aspects of the resin tissue of the pines, and his results already throw much light on the origin and character of the resin tissue in these forms.

† JEFFREY, 1905.

‡ JEFFREY, 1903.

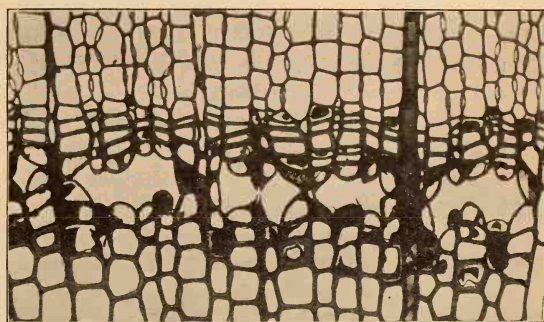
tangential association. The resemblance of the resin canals of *Araucariopitys* to those of the pine cone indicates that they are of a primitive type, since the conservatism of this region is now generally recognised. This form, then, from the character of its traumatic response, which is not of the "revival" type, cannot be a pine supposedly differentiating in the direction of the Araucarians, at such a stage that the resin canals are developed only in case of need.

The other feature referred to, which supports this view, is the relationship of resin canals to the spur shoot in both *Araucariopitys* and the living pine. A reference to figs. 65 and 68 (Plate 7) will make this point clear. The fact that the branch of *Pinus resinosa* from which the former figure comes was severely wounded nearer the main stem may not be without significance. The wounding in this case has "revived" the ancestral relationship to the spur shoot which is so clearly marked



TEXT-FIG. 5.

TEXT-FIG. 5.—*Araucariopitys americana*.  $\times 180$ . Traumatic Series of Resin Canals from JEFFREY, 1907, Plate 28, fig. 5.



TEXT-FIG. 6.

TEXT-FIG. 6.—*Abies amabilis*.  $\times 150$ . Traumatic Series of Resin Canals.

in *Araucariopitys*, a relationship which is only slightly indicated normally in the vegetable parts of the living pines (figs. 63 and 66), but which is often quite apparent in the cone (fig. 64, Plate 7). This relationship to the spur shoot is a suggestive one, and we may have in the deciduous spur shoot a factor which is responsible or at least has greatly influenced the production of resin canals in the pines. Be that as it may, the evidence presented is considered sufficient to show that the resin canals of *Araucariopitys* are not of the "revival" type, but suggests that they are in the process of *acquisition*. The absence of resin canals in *Woodworthia*, perhaps in vital connection but at least in association with its persistent and primitive spur shoot, affords additional evidence, when geologically considered, that this view is correct, since this, the more ancient form, should have more pine-like resin canals than *Araucariopitys* if the Araucarineæ have been

derived from the Abietineæ; even normal resin canals might quite logically be expected here, whereas neither traumatic nor normal are present, at least neither have been described. JEFFREY makes the traumatic revival of resin canals, as has been stated above, the crucial point in determining whether the other transitional features, pitting, medullary ray structure, etc., shall be interpreted as indicative of the derivation of Araucarineæ from the Abietineæ or the reverse. The facts presented above make it impossible to consider the resin canals of Araucariopitys as of the revival type.

Another feature which Prof. JEFFREY emphasises in his transitional forms is the presence of a spur shoot. This he considers "a primitive attribute of the coniferous stock," which "has persisted, at least in a vestigial form, in connection with the reproductive apparatus long after it has disappeared, or almost disappeared, in the vegetative axis of the living Conifers, with the exception of the very ancient genus *Pinus*" (1910 *a*, p. 331). In his extensive monograph on the Abietineæ he (1905) has marshalled the evidence in favour of the brachyblast theory of the ovuliferous scale, citing the vegetative parallel in the leaves of *Sciadopitys*, the teratological occurrence of vegetative shoots in place of the ovuliferous scale (p. 29), and finally going back to the Cordaiteæ, where he says, citing SCOTT as authority: "It is not difficult to trace homologies with that of the latter group if we regard the ovuliferous apparatus in the Conifers as consisting of a reduced and modified axillary shoot" (p. 23). It is evident that if the presence of a brachyblast in the cone of the Abietineæ postulates the ancestral presence of a vegetative spur shoot in this group, much more does the occurrence of its prototype in the Cordaitean cone involve the presence of a vegetative spur shoot in the more ancient group. There is, however, no evidence in the fossil remains of the Cordaiteæ even to suggest such a possibility.\* There is also a lack of evidence in the living forms themselves, of the ancestral presence of a vegetative spur shoot. In the seedling of no pine, Araucarian or other Conifer, is there a trace of such a structure. All the Conifer series have spirally arranged primordial leaves with a free lamina. These primordial leaves have a more primitive organisation than the adult foliage.† They persist in the pines for a year or more (in *Pinus canariensis* for many years), and can even be recalled in the adult in many forms by wounding (*Pinus rigida*, etc.). Strikingly in contrast to this is the fact that in none of the other Conifer forms does wounding revive a spur shoot. The spur shoot of the pines must thus be considered of a cenogenetic character. That of *Woodworthia* of the Triassic, which is very persistent and bears many leaves, is clearly of a primitive type—might well be that of an Araucarian in the initial stage of this branch specialisation, a specialisation which, together with its

\* The writer wishes it to be understood that he is not trying to refute the brachyblast theory (see THOMSON, 1909 *b*) of the cone scale, but only the inference which Prof. JEFFREY draws from it with regard to the presence of a vegetative spur shoot.

† COULTER and CHAMBERLAIN, 1910, p. 222.

more highly organised wood structure, may be considered to have made the pines of to-day the dominant group of the Conifers.

In conclusion, according to the theory which regards the Abietineæ as the ancestors of the Araucarineæ, we must look upon *Woodworthia* as having had ancestrally in the normal condition pine-like pitting on the tracheids, pine-like medullary ray structure and pine-like resin canals, both horizontal and vertical, in the secondary wood. The difficulties which beset this position, even when the Abietineæ were thought to extend to the Carboniferous, are apparent when one considers the relatively short period in which the loss of Abietinean features must have taken place. Between the Triassic and the Carboniferous there is only the Permian, which, I believe, geologists to-day are inclined to view as a part of the Carboniferous. Further, if it be granted that the Abietineæ have been derived from the Cordaitan alliance, this process would also have to be completed, that is pines fully developed from Cordaitan forms, in the earlier part of this same period. Thus the wood of the Araucarineæ, which is practically identical in structure with that of the Cordaitales, must have been transformed into *pine-like* wood and then have acquired its original structure again. To one who appreciates the conservatism of anatomical details the geological time is too limited for the several important and unrelated details involved to undergo this "double transformation."

The time, too, becomes the shorter the farther back geologically the Araucarineæ are traced and the farther forward the place of origin of the Abietineæ from the Cordaitales is put. Two forms were considered important by JEFFREY as indicating the Carboniferous age of the Abietineæ, *Pityoxylon chasense* and *P. Conventzianum*.<sup>\*</sup> Both forms have recently been shown not to be authentic—the former structurally† and the latter geologically.‡ There is at present no evidence of any Abietinean form either in or earlier than the Triassic, where *Woodworthia*, the first Araucarian supposed to have been derived from the Abietineæ, makes its appearance. Thus the geological history, as the evidence stands at present, has fulfilled SEWARD's prediction of 1906§ that "further research will strengthen the view that palæontological records point to the Araucarineæ as superior in antiquity . . . to the Abietineæ." It further substantiates the view of the transitional fossil forms which, from the standpoint of the transitional features themselves, have been considered as indicating that either the Araucarineæ are the parental stock from which the Abietineæ have been derived, or that both families are of independent origin from the Cordaitalean alliance. This view, too, must hold until authentic Abietinean forms are found sufficiently far back geologically to allow time for the "double transformation" which the Abietinean theory of the ancestry of the Araucarineæ demands.

\* JEFFREY and CHRYSLER, 1906.

† THOMSON and ALLIN, 1912.

‡ GOTHAN, 1910, p. 22.

§ SEWARD and FORD, 1906, p. 384.



## 10. GENERAL RESULTS.

1. There are two recent views of the ancestry of the Araucarineæ, the Lycopod which has been advanced by SEWARD and the Abietinean by JEFFREY. The result of the present work confirms the old view of the derivation of the group from the Cordaitalean alliance.

2. Leaf gaps are present in the stem, and their ancestral presence is indicated by their occurrence in the cone and seedling. The leaf gap is considered to be of fundamental importance as indicating that the Araucarineæ have been derived from Pteropsid and not Lycopsid stock.

3. In leaf morphology, habit, and structure the Araucarineæ resemble the Cordaitalean forms. This is especially true of the double and multiple leaf traces in the secondary wood, which find a parallel in no other group of the Gymnosperms.

4. The ordinary radial pitting of the tracheids is Cordaitalean, the character of this in the cone recalling even the more primitive forms of this alliance. The ray pitting of the tracheids is even more primitive than the above and a contrast to the specialised condition of the pine alliance.

5. The resin tissue of the secondary wood of the Araucarineæ consists of resinous tracheids associated with the medullary rays, and of parenchyma derived from tracheary tissue. That of the pines is formed in a similar way, but has become more specialised, both the rays and the wood having developed resin canals from aggregates of resin cells. In the root and cone axis, however, resin tracheids are found like those in the Araucarineæ. The Araucarineæ are the basal forms which indicate how the resin tissue in the other modern Conifers has been derived from their Cordaitalean ancestors.

6. The medullary rays consist of thin-walled unpitted parenchyma, without typical ray tracheids, though bent-ended tracheids are associated with the rays. These are probably the precursors of the ray tracheids, since they have been found in the Cordaitalean forms and in the cone axis of the pines. The ray cells are practically identical with those of the Cordaitalea.

7. The rays of the bast have no albuminous cells, which are the counterparts of the ray tracheids in such forms as have this specialisation of the rays.

The periderm is late in development in the stem, a fact possibly associated with the persistent leaf base.

8. The state of development of the growth rings varies in the different species and even in different individuals of the same species. Whether these are *annual* rings has not been determined. They are often "inverse" or even root-like. Normal rings also occur, so that the Araucarineæ combine the characteristics of the growth ring of the ancient and of the modern forms. Tangential pitting occurs where the growth ring is well developed. It is usually multi-seriate and sometimes flattened.

9. The transitional features of JEFFREY'S fossil "Abietinean-Araucarian" forms

indicate the derivation of the former from the latter. This view is upheld by the greater geological age of the Araucarineæ, the Permian and Carboniferous forms of the Abietineæ having recently been shown not to be authentic.

#### 11. ACKNOWLEDGMENTS.

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## DESCRIPTION OF PLATES.

## PLATE 1.

- Fig. 1.—*Araucaria imbricata*. Transverse of Young Stem.  $\times 40$ . Cortex below with numerous mucilage ducts and sclerotic cells, the latter especially abundant around the leaf trace. Sclerotic cells in medulla also.
- Fig. 2.—*A. imbricata*. Transverse of Young Stem.  $\times 225$ . A sclerotic cell with calcium oxalate crystals.
- Fig. 3.—*A. Bidwillii*. Transverse Section of Mucilage Duct from the Cortex of the Cone.  $\times 80$ .
- Fig. 4.—*A. imbricata*. Transverse of Young Stem.  $\times 80$ . Leaf gap with sclerotic cells in it and also accompanying the trace.
- Fig. 5.—*A. imbricata*. Transverse of Cone Axis.  $\times 25$ . Medulla above with mucilage ducts. Two sporophyll traces below (*sp. t.*<sup>1</sup>, *sp. t.*<sup>2</sup>), in the cortex, the one to the right with a mucilage duct in its gap.
- Fig. 6.—*A. Bidwillii*. Transverse of Epicotyl.  $\times 80$ . Leaf gap above the primordial leaf trace to the lower right. Above, the so-called "false trichotomy of a second leaf trace."
- Fig. 7.—*Agathis australis*. Transverse of Cone Axis.  $\times 35$ . Sclerotic nests (*sc. n.*) in medulla (from "revived" material).
- Fig. 8.—*A. Moorei*. Transverse of Root.  $\times 35$ . Primary wood diarch; four mucilage ducts in the cortex, while bounding it is the sclerotic tissue in a sheath.
- Fig. 9.—*Araucaria excelsa*. Transverse of Root.  $\times 80$ . One arc of the primary wood, the solid metaxylem (*a*) above and the protoxylem (*b*) in a nest of parenchyma below.
- Fig. 10.—*A. excelsa*. Radial of Root.  $\times 80$ . Protoxylem in the centre of the figure, metaxylem to the left, and secondary wood to the right.



## PLATE 2.

- Fig. 11.—*A. excelsa*. Longitudinal of Metaxylem of Root.  $\times 80$ . Pitting alternate, 2-seriate and flattened on one element to the left of the figure, the rest pseudo-scalariform.
- Fig. 12.—*A. excelsa*. Longitudinal of Root.  $\times 80$ . Short metaxylem elements to the left, a lateral root coming off at the right.
- Fig. 13.—*Agathis Moorei*. Transverse of Leaf.  $\times 220$ . The section is from the middle of the leaf, and shows a multiple palisade. The vein has transfusion tissue on its flanks but no centripetal xylem.
- Fig. 14.—*Araucaria brasiliensis*. Transverse of Leaf Tip.  $\times 35$ . Sclerotic hypodermal strands well developed and veins with much transfusion tissue and centripetal xylem—the lighter tissue above the veins.
- Fig. 15.—*A. imbricata*. Tangential of Branch.  $\times 35$ . Single leaf trace in wood about three years old.
- Fig. 16.—*Agathis bornensis*. Tangential of Branch.  $\times 80$ . Double leaf trace in wood about three years old.
- Fig. 17.—*A. spinulosa*. Transverse of Branch.  $\times 35$ . The central parenchyma at the top of the section is just at the medulla. The two indentations of the cortex mark the two bundles of the trace, which, nearer the pith, are still separated ( $b^1$  and  $b^2$ ) by secondary wood ( $x^2$ ).
- Fig. 18.—*Mesoxylon Sutcliffei*. Transverse of Stem.  $\times 15$ . (a) Double trace bundles separated by secondary wood. (b) Six trace bundles in the cortex, the outer pairs just forming.
- Fig. 19.—*Agathis pumila*. Tangential of Stem.  $\times 18$ . Two large bundles of a trace ( $a$  and  $c$ ) accompanied by two smaller ones ( $b$  and  $d$ ).
- Fig. 20.—*Dadoxylon Brandlingii*. Tangential of Stem.  $\times 50$ . One of the six bundles of the trace (McGill University Collection).

## PLATE 3.

- Fig. 21.—*Agathis Moorei*. Transverse of Branch.  $\times 35$ . Double trace, one bundle in advance of the other.
- Fig. 22.—*Araucaria Bidwillii*. Transverse of Epicotyl.  $\times 35$ . Three leaf traces: that to the left single, to the lower right triple, and to the top pentad.
- Fig. 23.—*Agathis australis*. Transverse of Cotyledonary Node.  $\times 25$ . Traces of each of the two cotyledons double, with the component bundles of each far apart and leaving the stem cylinder slightly in advance of one another.
- Fig. 24.—*A. bornensis*. Radial of Branch.  $\times 225$ . Scalariform pitting retained at the ray longer than elsewhere on the tracheid.
- Fig. 25.—*A. bornensis*. Radial of Branch.  $\times 225$ . The initial stages in the transition from scalariform to multi-seriate bordered pits are very clear, the pits opposite or alternate according to the type of scalariform.

- Fig. 26.—*A. bornensis*. Radial of Branch.  $\times 225$ . Older wood with multi-seriate medullary ray pitting and uni-seriate tracheary, the former much larger than the latter.
- Fig. 27.—*Dadoxylon materiarium*. Radial of Stem. (a)  $\times 120$ , (b)  $\times 180$ . Terminal pitting, alternate and opposite (X). Ordinary pitting reduced, often 1-seriate or absent.
- Fig. 28.—*Araucaria Cookii*. Radial of Root.  $\times 225$ . Elongated four-armed cells of the rays. Transitional pitting retained much longer than in the stem.
- Fig. 29.—*A. Cookii*. Radial of Root.  $\times 225$ . More mature ray pitting, 3- to 4-seriate. Note the vertical fusion of two pits near the centre of the figure. The pit opening normally is elongated and obliquely placed.
- Fig. 30.—*A. Bidwillii*. Radial of Cone Axis.  $\times 225$ . Rays oblique, as in the root. Scalariform pitting very marked at the rays to the left, after the multi-seriate has been established. On the second tracheid to the right, between the pits, there is seen an appearance of a bar of Sanio. Cf. also figs. 24 and 28.

## PLATE 4.

- Fig. 31.—*A. Bidwillii*. Radial of Cone Axis.  $\times 225$ . Showing the transitional scalariform to reticulate pitting on the tracheid wall where it touches another tracheid. The scalariform framework is very evident and the vertical bridges by which the separate pits are formed. There are certain resemblances to bars of Sanio here also.
- Fig. 32.—*A. Bidwillii*. Radial of Cone Axis.  $\times 35$ . Spiral tracheids to the right. About the middle the beginning of the transitional secondary wood.
- Fig. 33.—*A. Bidwillii*. Part of fig. 32.  $\times 225$ . At the upper left a scalariform element with very large bars.
- Fig. 34.—*A. bidwillii*. Radial of Cone Axis.  $\times 360$ . 3- to 5-seriate pitting, pits with oblong pore.
- Fig. 35.—*Agathis bornensis*. Tangential of Stem.  $\times 360$ . Tangential pits of summer wood in face view, the radial in section.
- Fig. 36.—*Larix americana*. Radial of Root.  $\times 360$ . (a) Tri-seriate pits and no bars of Sanio. (b) Bi-seriate and bar of Sanio attached to the pit margin. (c) Bars as in (b) and pits flattened, opposite and alternate.
- Fig. 37.—*Agathis bornensis*. Radial of Branch.  $\times 360$ . Single row of pits with rudimentary bar of Sanio and no torus.
- Fig. 38.—*Araucaria Cookii*. Radial of Root.  $\times 225$ . Ordinary pitting bi-seriate or none, medullary ray pitting 2- to 3-seriate, with oblique oblong pore. To the lower right a "fusion" pit.

- Fig. 39.—*Cycas revoluta*.—Tangential of Stem.  $\times 225$ . Pits without torus, as in fig. 35.
- Fig. 40.—*Agathis bornensis*. Transverse of Branch.  $\times 225$ . The annual (?) ring and deposits of resin in the tracheids along the medullary rays.
- Fig. 41.—*Agathis robusta*. Radial of Old Stem.  $\times 225$ . Various forms of resin deposit in the tracheids.
- Fig. 42.—*Pityoxylon* sp. Radial of Stem.  $\times 360$ . Pits with bars of Sanio, oblique pores and torus.

## PLATE 5.

- Fig. 43.—*Dadoxylon materiarium*. Transverse of Stem.  $\times 80$ . Deposit in tracheids in radial rows, the central row beside a ray.
- Fig. 44.—*Agathis australis*. Radial of Old Stem. (a)  $\times 225$ . Resin deposits in medullary ray cells and in tracheids adjacent to the ray. (b)  $\times 360$ . The deposit lines the tracheid far above and below the bridges. The wall is locally thickened where the deposit occurs.
- Fig. 45.—*Araucarioxylon* sp. Transverse of Stem.  $\times 80$ . Deposit in tracheids along the rays.
- Fig. 46.—*Dadoxylon Brandlingii*. Oblique Tangential of Stem.  $\times 225$ . Meniscus-like deposits in the tracheids.
- Fig. 47.—*Agathis australis*. Tangential of Old Stem.  $\times 360$ . Various forms of resin deposit.
- Fig. 48.—*Araucarioxylon* sp. Radial of Stem. (a)  $\times 80$  and (b)  $\times 120$ . Various forms of deposit in tracheids.
- Fig. 49.—*Agathis bornensis*. Tangential of Stem.  $\times 360$ . Septate tracheids on outer border of summer wood.
- Fig. 50.—*A. bornensis*. Radial of Stem.  $\times 225$ . A sclerotic cell, about the centre of the upper part, below which is parenchyma; coterminous with the tracheids in the same radial row. The boundary between the two is at "a."
- Fig. 51.—*A. Moorei*. Transverse of Root.  $\times 360$ . The central row of tracheids to the left is replaced by two, and the third element of the upper row is a parenchyma cell.
- Fig. 52.—*A. bornensis*. Radial of Stem.  $\times 225$ . Resin deposit very abundant.

## PLATE 6.

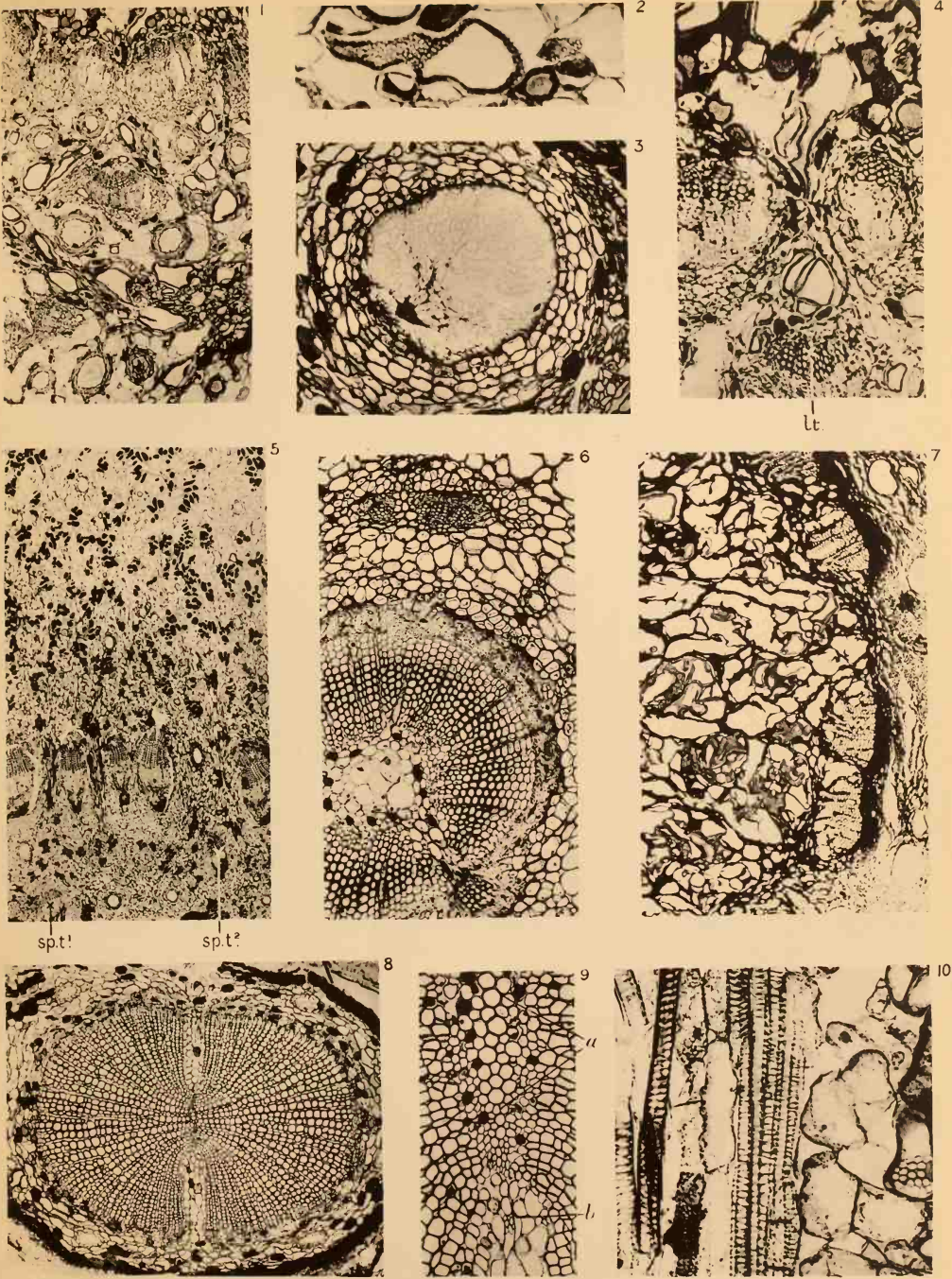
- Fig. 53.—*Agathis australis*. Transverse of Branch.  $\times 80$ . Sclerotic cells of the pith continued into the medullary rays in connection with the exit of the foliar trace.
- Fig. 54.—*A. australis*. Transverse of Branch.  $\times 225$ . To show details of pitting of sclerotic cells.

- Fig. 55.—*Araucaria Cookii*. Transverse of Root.  $\times 360$ . Beginning at "a" a series of seven walls can be seen, so pitted and arranged that radial flow can be effected.
- Fig. 56.—*Amyelon radicans*. Transverse of Root.  $\times 35$ . Growth ring. From English Coal Measures.
- Fig. 57.—*Araucarioxylon*, *sp.* Transverse of Stem.  $\times 80$ . Growth ring with darker contents in the summer tracheids.
- Fig. 58.—*Agathis bornensis*. Tangential of Stem.  $\times 360$ . Tangential pitting 1- to 2-seriate and flattened. The thinness of the walls of the ray cells is indicated and the unilateral bordered pitting of the tracheid where it touches the rays (*a* and *b*).
- Fig. 59.—*Agathis Bidwillii*. Transverse of Branch.  $\times 225$ . "Spring" wood in the centre, bounded outside and inside (below in the section) by "summer" wood, the outer having some tangential pitting, and so simulating the more an "inverse" growth ring.
- Fig. 60.—*A. Bidwillii*. Transverse of Branch.  $\times 225$ . Root-like growth ring (up is towards the outside).

## PLATE 7.

- Fig. 61.—*Pinus austriaca*. Transverse of Stem.  $\times 20$ . After a second severe double wound. The resin canals are increased 7-8 times the normal number calculated per square centimetre. The traumatic resin canals are occluded.
- Fig. 62.—*Pinus austriaca*. Transverse of Stem.  $\times 35$ . Quarter way round the stem to show the extent of the influence.
- Fig. 63.—*Pinus Strobus*. Transverse of Twig.  $\times 150$ . At the left of the spur shoot trace is a resin canal and a tangential series of parenchyma cells.
- Fig. 64.—*Pinus resinosa*. Transverse of Cone Axis.  $\times 170$ . A series of five resin canals is associated with the exit of the brachyblast trace.
- Fig. 65.—*Pinus resinosa*. Transverse of Branch.  $\times 35$ . Above four Podapion galls. There is a tangential series of resin canals in the second year associated with the exit of the vascular supply of the spur shoot.
- Fig. 66.—*Pinus Strobus*. Transverse of Branch.  $\times 50$ . Three canals above the spur shoot trace.
- Fig. 67.—*Pinus palustris*. Transverse of Cone Axis.  $\times 15$ . Loose tangential series of resin canals.
- Fig. 68.—*Araucarioxylon americana*. Transverse of Branch.  $\times 25$ . The spur shoot bundle has a lax tangential series of resin canals associated with it.



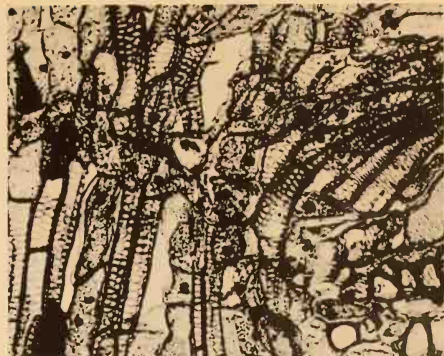








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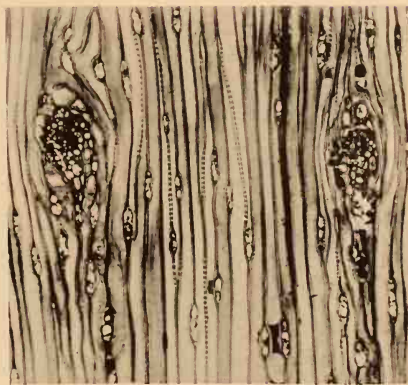
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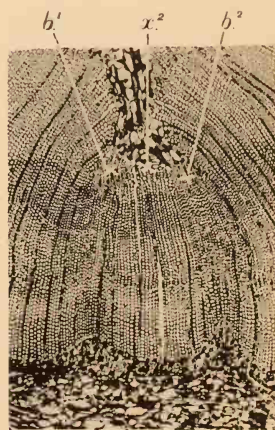
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15



16



17



18<sup>a</sup>



18<sup>b</sup>



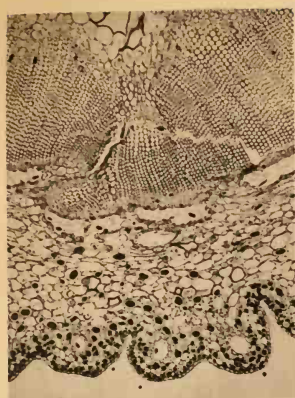
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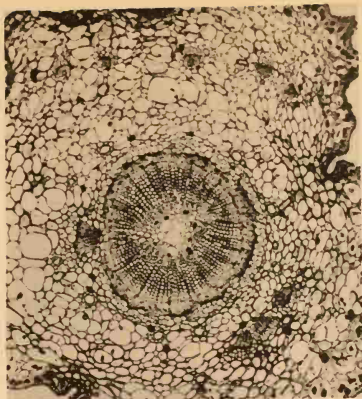
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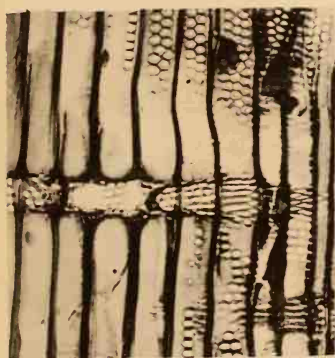
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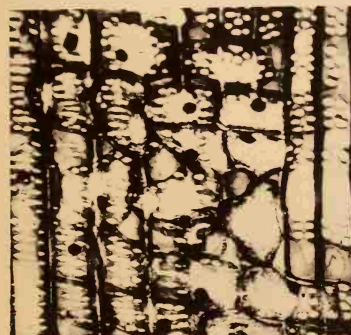
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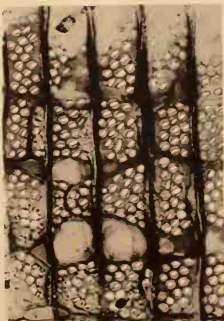
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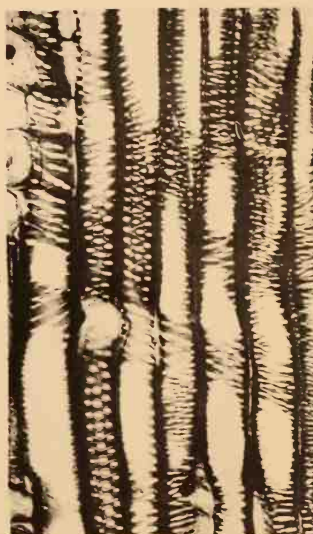
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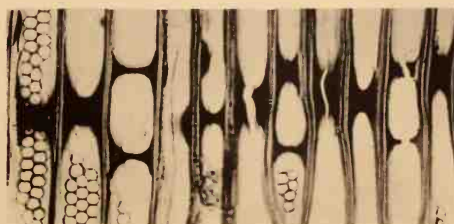
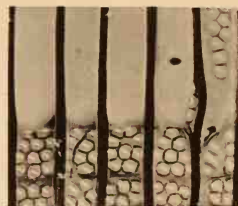
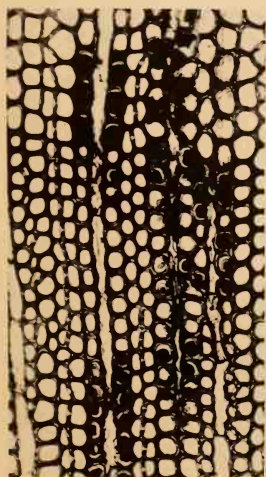
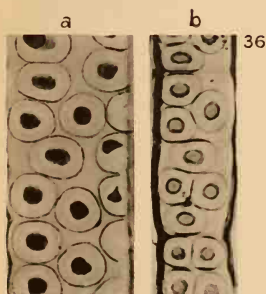
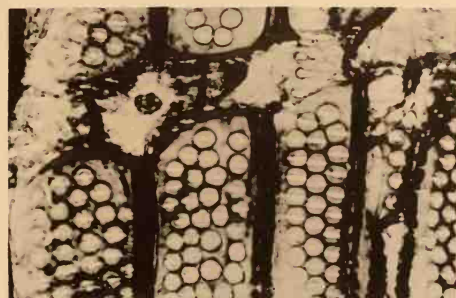
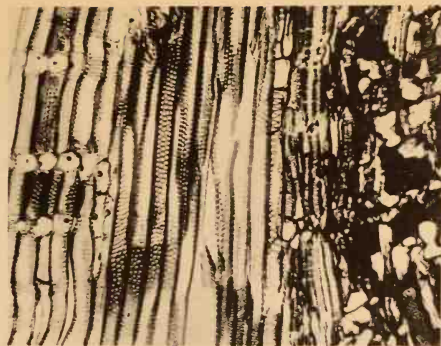
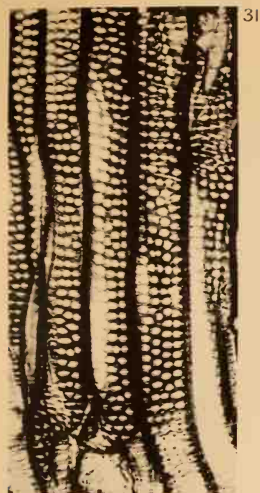
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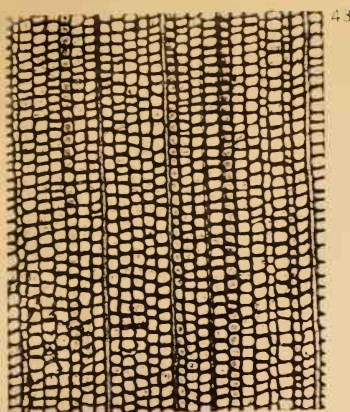




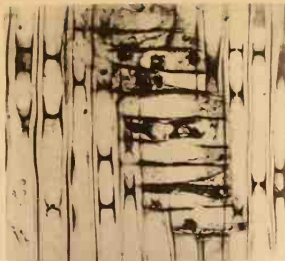




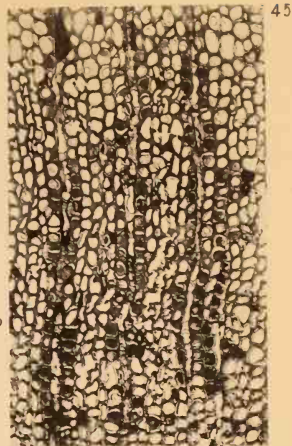




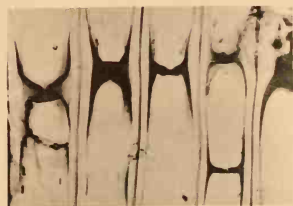
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44a



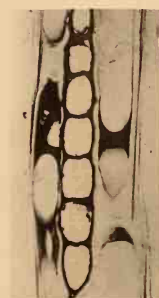
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44b



46



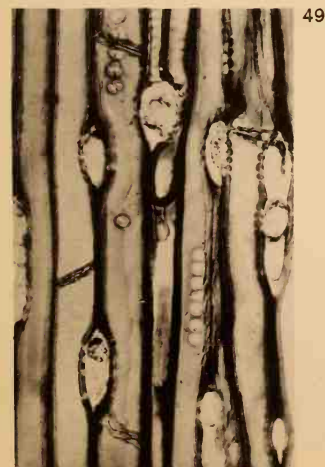
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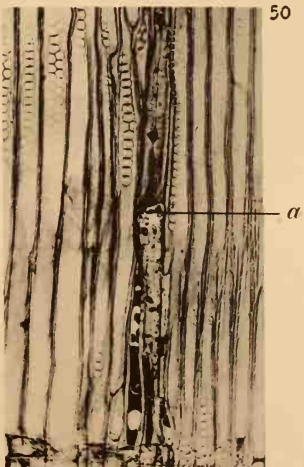
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48b

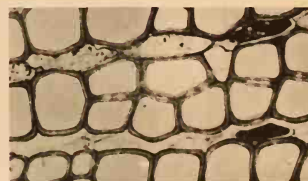


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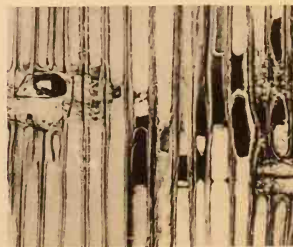


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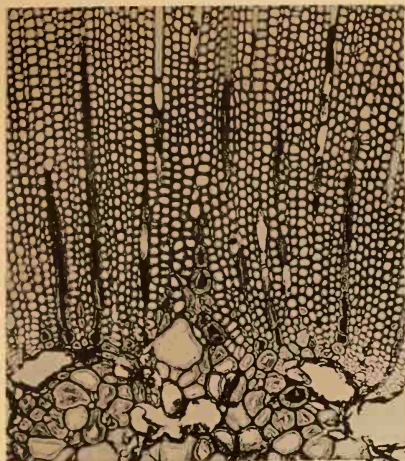
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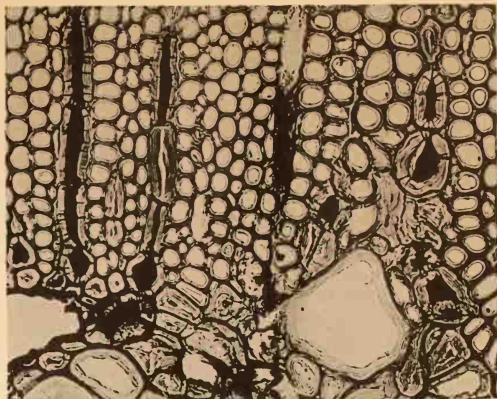
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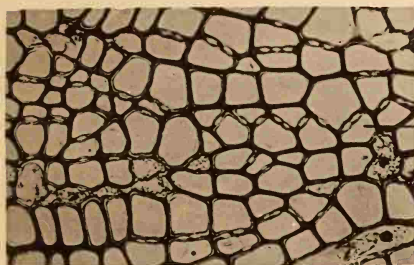




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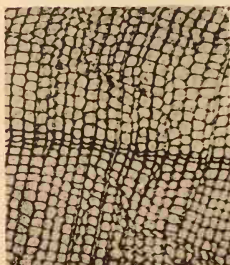


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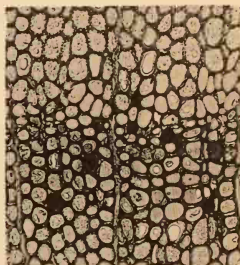


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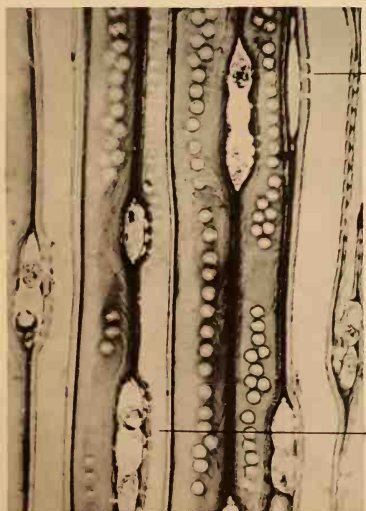
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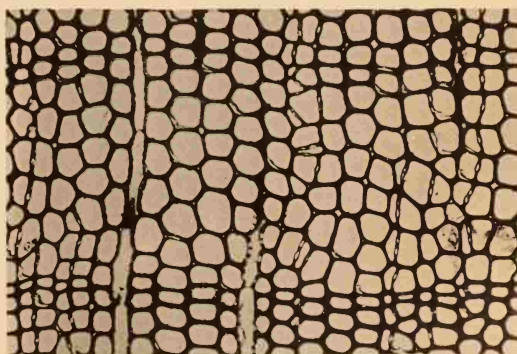
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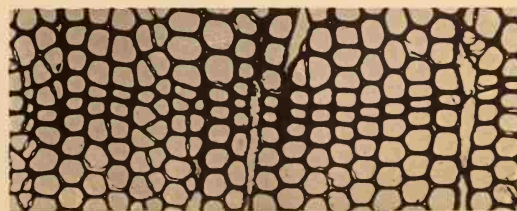
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*a*

*b*



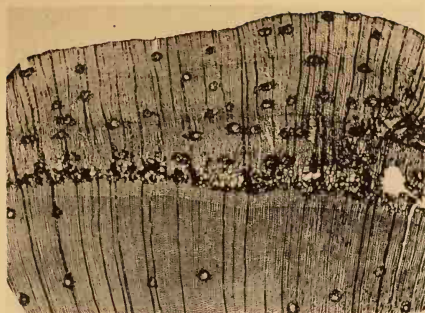
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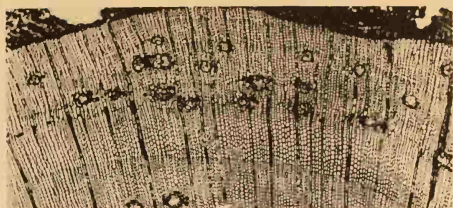
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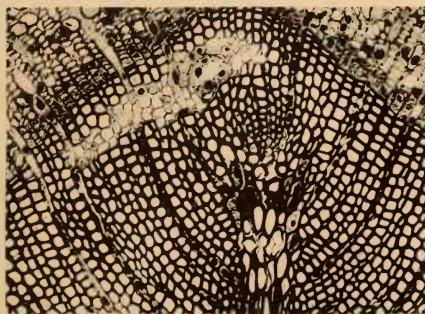




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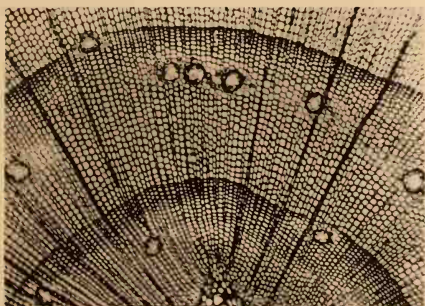
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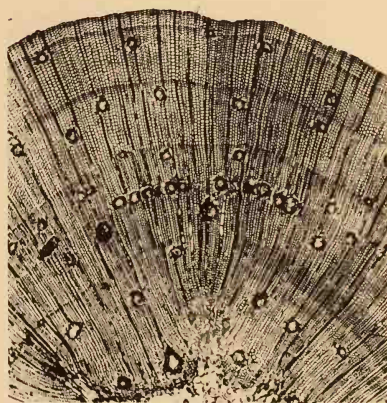
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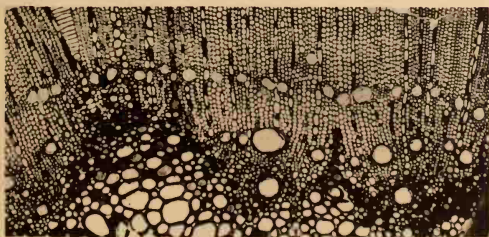
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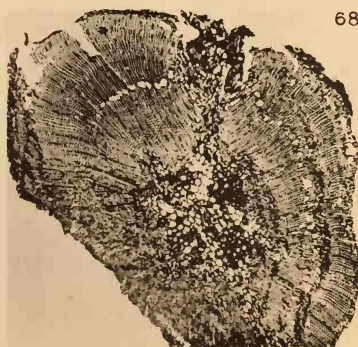
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